BIOLOGY OF THE RABBIT (ORYCTOLAGUS CUNICULUS (L.)) IN CENTRAL OTAGO, NEW ZEALAND, WITH EMPHASIS ON BEHAVIOUR AND ITS RELEVANCE TO POISON CONTROL OPERATIONS

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CONTENTS

ABSTRACT

This research arose from concern over declining success rates of rabbit poisoning operations in Central Otago. It consisted of a detailed study of behaviour in a natural population of rabbits which was subsequently poisoned. The aim was to test the hypothesis that social behaviour and the existence of neophobia could be contributing to control operation failures. Several other aspects of rabbit biology in Central Otago were investigated including population age and sex structure, growth and condition, and reproduction.

Information on rabbit behaviour was obtained from intensive observation of a population of 50-100 rabbits over a period of two years. Activity budget results for the period of peak emergence (late afternoon-early evening) revealed similar patterns to those recorded previously, with some minor differences in the classification of individual behaviours. Social organisation varies seasonally and spatially, with a range of social structures present at any one time. Heterogeneity of the habitat, in particular the patchiness of the food supply, influenced spatial and temporal features of social organisation. Reproductive efficiency and optimal use of resources appear to be important determinants of social structure; the concept of economic defendability is relevant. Activity range size and shape were extremely variable with female rabbits generally having larger ranges than males. Some relationship between activity range size and metabolic requirements and economic defendability was evident. Gross movement patterns were a product of habitat heterogeneity and the limited availability of permanent resting locations because of the unsuitability of the substrate for burrowing.

Age structures of rabbit populations in Central Otago are characterised by relatively few individuals greater than 24 months old; this suggests high mortality and a rapid turnover rate. Growth and condition results reflect some measure of environmental conditions in Central Otago. Seasonal variation in

fat-related condition suggests hormonal control of fat reserves rather than regulation by resource availability. The breeding season is sharply defined, a product of severe and strongly seasonal environmental conditions. Annual productivity is about 22 young per female.

Evidence is presented for the existence of neophobia in Central Otago rabbit populations. Despite the genetic basis for this trait, environmental factors may influence an individual's propensity to exhibit neophobia. This may account for the considerable variation in neophobic responses among individual rabbits.

1 GENERAL INTRODUCTION

1.1 Taxonomic and historical background

The European rabbit **Oryctolagus cuniculus** (L.) belongs to the Family Leporidae of the Order Lagomorpha, which also includes the hares and pikas. Although they were originally classified within the Order Rodentia, lagomorphs are now considered to be an isolated offshoot of early eutherian stock, whose similarities to the rodents may only be superficial (Colbert 1980). Electrophoretic studies on blood proteins confirm the phylogenetic distinction of lagomorphs, and show no relationship between lagomorphs and rodents (Walker 1964).

The original range of the rabbit was the Iberian peninsula (Zeuner 1963). Through introduction by man the species now inhabits many other continents and islands including Australia, New Zealand, most of Europe including Great Britain, and several parts of the United States and South America. In many of these new habitats rabbit populations increased rapidly in the absence of natural predators and quickly reached pest proportions. Domestication was responsible for much of the early spread in Europe, although many of the present domesticated breeds differ markedly from the original wild stock (Walker 1964).

1.2 The rabbit in New Zealand

From 1838 to the late 1850s there were numerous liberations of wild rabbits in New Zealand for sport, most of which were unsuccessful. However, they finally became established in the 1860s and spread rapidly in association with sheep farming (Howard 1959). By the 1870s the rabbit had become a major agricultural pest in the southern part of the South Island (Wodzicki 1950). In several areas, particularly the semi-arid regions of Central Otago, they remain a serious pest of pastoral agriculture and soil conservation (Kerr et al. 1983). Although they occupy most suitable habitats throughout New Zealand,

many areas now contain less rabbits than previously, mainly due to changes in land management practices (Bull 1956, Howard 1963, Williams 1977, Bell and Williams 1981).

A considerable amount of ecological research has been carried out since 1948 by Animal Ecology Division of the Department of Scientific and Industrial Research with the aim of providing a broad understanding of rabbit biology in New Zealand. This research includes investigations on parasites (Bull 1953a, 1953b, 1958, 1964), reproduction and mortality (Tyndale-Biscoe and Williams 1955, Watson 1957, Bull 1962, McIlwaine 1962), ageing and marking methods (Tyndale-Biscoe 1953, Watson and Tyndale-Biscoe 1953) and population regulation (Howard 1959, Gibb et al. 1969, 1978). Even more work has been done over the same period in Australia, where the rabbit is also an important agricultural pest. Recent research by Ministry of Agriculture and Fisheries (MAF) scientists has concentrated on aspects related to the control operations currently used to reduce rabbit numbers (Bell 1979, Williams 1983). Most of this work has been carried out in Central Otago at the request of the Agricultural Pests Destruction Council (APDC) which is concerned at the continuing high cost of control in the area, partly due to the relatively low success rate of poisoning operations (Agricultural Pests Destruction Council 1974).

1.3 History of rabbit control in New Zealand

A variety of methods has been employed over the years to reduce rabbit numbers in New Zealand. In the 1880s and 1890s large numbers of ferrets **Mustela furo**, stoats **M. erminea**, weasels **M. nivalis**, and cats **Felis catus** were released in an attempt to achieve biological control. Although these predators are widespread today, there is no evidence that they are effective in reducing rabbit numbers in the main problem areas (Wodzicki 1950, Howard 1959). However, research in both Australia (Myers and Schneider 1964) and New Zealand (Gibb et al. 1969, 1978) has shown that rabbit populations at

low densities may be regulated by predators. In the early years rabbit-proof fences were erected, especially in the South Island, in an unsuccessful attempt to halt the spread of rabbits. Gin trapping and poisoning using arsenic, phosphorus, and strychnine were common until the early 1950s. Significant disadvantages were associated with both arsenic and strychnine, which are extremely stable poisons, therefore preventing restocking until long after an area had been poisoned.

Since the 1950s sodium monofluoroacetate (compound 1080) has been the predominant poison used for rabbit control in most areas of New Zealand. Poisoning with 1080 on carrot, oat, or pollard baits takes place in autumn and winter months, while night shooting from vehicles occurs at all times of the year. The main advantages of 1080 poison are that it is water soluble and easily applied to baits, biodegradable and does not persist on the pasture, and relativity specific in its toxicity. Therefore it presents minimal risk to non-target species (Batcheler 1978, Rammell and Fleming 1978). Over the same period the widespread use of small aircraft has permitted the application of large quantities of poison bait to previously inaccessible areas.

Since the goal of extermination was abandoned in 1971 in favour of a policy of sustained control, more emphasis has been placed on gaining a thorough knowledge of the ecology of the rabbit in order to improve the efficiency of field operations (Gibb et al. 1978). In spite of this large amount of research, rabbits continue to be an agricultural pest, not only in Central Otago but in several other areas of New Zealand as well.

Successful control depends upon the reduction of rabbit numbers to a level where they no longer pose an economic threat. Although this goal is often reached in the short term, the crux of the problem lies in the size of the residual population and its capacity for resurgence following poisoning (Rowley 1968). The rabbit has a high level of fecundity, the average number of young produced by a female in one season being 20-40 depending on habitat (Watson 1957, Bell 1977, Williams 1983). This high rate of productivity

confers upon the rabbit an amazing ability to recover from control campaigns when natural mortality is low. Consequently, for any lasting effect over 90% of the population must be killed in a control operation (Carrick 1957).

The current cost of rabbit control is over $12 million annually with approximately 19% of this total being spent in the Central Otago region (Agricultural Pests Destruction Council 1984). The recent review of the pest destruction industry (James et al. 1983) and proposed shift in emphasis towards a more cost-efficient approach to rabbit control (Williams 1977, 1983, Bell and Williams 1981, Kerr et al. 1983) highlights the need to apply current scientific knowledge when formulating control strategies. Over large areas of New Zealand rabbit populations are stable and at low densities, and continued control in these areas will not contribute to increased agricultural production.

1.4 The present control situation in Central Otago

Current rabbit numbers in Central Otago are considerably less than several decades ago, but they remain a serious problem over many parts of the region. A substantial proportion of Central Otago is land with an 'extreme' or 'high' rating of rabbit proneness, including 50% of the area within the Alexandra Pest Destruction Board district (Kerr et al. 1983). Although the annual productivity of female rabbits is relatively low compared with other areas of New Zealand, due to a shorter breeding season, the environment in Central Otago is ideal resulting in greater survival of young rabbits. The rabbit problem is greatest on land with an inherently low productive capacity (Kerr et al. 1983); therefore, the cost-effectiveness of control operations is often questionable.

Several favourable years for rabbit breeding and survival in Central Otago, combined with proposed decreases in government funding of pest destruction, has highlighted the degree of the problem in this region. The result has been a concerted effort by the farming sector in Central Otago for

the reintroduction of the viral disease myxomatosis. Previously, myxomatosis-infected rabbits were released at a number of trial sites in New Zealand in the early 1950s (Filmer 1953) but the disease failed to establish within rabbit populations because suitable insect vectors were absent.

Poison operations in Central Otago often leave about 30% of the population alive and numbers may return to their previous levels in only one year. The problem is compounded by the tendency for older rabbits to survive poison operations in disproportionate numbers (J Bell pers. comm.), thus facilitating rapid population increase by experienced breeders.

Recent research in this region (Bell 1979) and Western Australia (Oliver et al. 1982) suggests that rabbit behaviour could be the main factor responsible for low rates of success in control campaigns. Deficiencies in the poisoning technique and an increase in the tolerance of rabbits to 1080 were eliminated as major causes of these poor results. In Western Australia, where poison trials have been carried out since 1958, it appears that the effectiveness of 1080 poisoning campaigns is declining. The reason proposed for this decline, and possibly the low success rates of Central Otago poison control operations, is the selection for rabbits exhibiting neophobia (fear of new objects in familiar places, Chitty and Shorten 1946) since the advent of 1080 poisoning in the 1950s.

1.5 Aims of the study

The rabbit is a significant pastoral pest in Central Otago, and this research focuses upon possible reasons for the increasing frequency of control operation 'failures' in the region. The possibility that the social behaviour of rabbits could affect taking of poison baits (therefore biasing the age, sex, and social structure of the surviving population), and that rabbits with a neophobic reaction to baits are being selected for, were the dominant themes of investigation. The study concentrated on a single, easily observed population. A very detailed picture of the population's behavioural repertoire

provided the necessary base of information from which the subsequent responses of individual rabbits to a poison operation could be interpreted. It was hoped to provide clues as to why some rabbits are now avoiding baits, as well as gain clear evidence of neophobic behaviour.

Since no other detailed studies of rabbit behaviour have been undertaken in New Zealand, the information obtained was of considerable comparative value to previous studies in Great Britain and Australia. As behaviour is influenced by an animal's condition and circumstances, it was necessary to obtain regular samples of rabbits for autopsy and the determination of a range of biological indices.

The study was carried out in Central Otago, within the Alexandra Pest Destruction Board district. Behaviour investigations and the poisoning experiments took place near Butchers Dam, 10 km south of Alexandra. Autopsy samples were obtained from a range of localities, all within the area controlled by the Alexandra Pest Destruction Board. The research program consisted of:

1 A detailed study of rabbit behaviour, especially the social behaviour of the population, over a period of two years.
2 Poisoning of the study population to determine whether social behaviour influences control results and whether rabbits exhibit a neophobic reaction to baits.
3 Collection of monthly samples of rabbits for determination of age structure, reproductive indices, and a range of condition indices.

Although these three lines of investigation are interrelated, they are dealt with in separate sections. A final chapter attempts to integrate these findings and presents an overall discussion of the problem and some relevant implications for future rabbit control strategies.

2 STUDY AREA

2.1 Location

The precise geographical boundaries of Central Otago are hard to define, but it is usually accepted that the region consists of several broad basins which run generally in a northeast to southwest direction, and lie between wide, gently-graded ranges of hills and mountains (Figure 2.1). Extensive pastoral farming is the predominant type of agriculture over most of Central Otago, with stone and pip fruit orchards occurring close to rivers and streams where soils are suitable and irrigation possible. Along the major rivers scoured out hollows and numerous dredge tailings survive as relicts from the gold mining era of the 1860s.

Within Central Otago the Alexandra Pest Destruction Board district covers an area of approximately 175,000 hectares. The district's boundaries are the Old Woman Range and Old Man Range in the west, the Knobby Range in the south, and the Raggedy Range and southern parts of the Rough Ridge in the east. Lauder Creek, originating in the Dunstan Mountains, marks the northern boundary of the district (see Figure 2.1).

The Butchers Dam research area is situated about 10 km south of Alexandra (45°S 169°E) on the southern edge of one of the main basins of Central Otago (see Figure 2.1). It consists of approximately 200 ha of Crown Land bounded by Butchers Dam and Butchers Creek in the west and Lake Roxburgh in the east (Figure 2.2). The area has been leased from the Crown by the APDC for the Ministry of Agriculture and Fisheries' Rabbit Research Group and has remained unstocked for the past decade. The last rabbit control operation on the area was carried out in June 1973.

2.2 Physiographic description

The mountains of Central Otago rise to over 1800 m while most of the foothills and valley floors are at elevations between 300 m and 600 m.

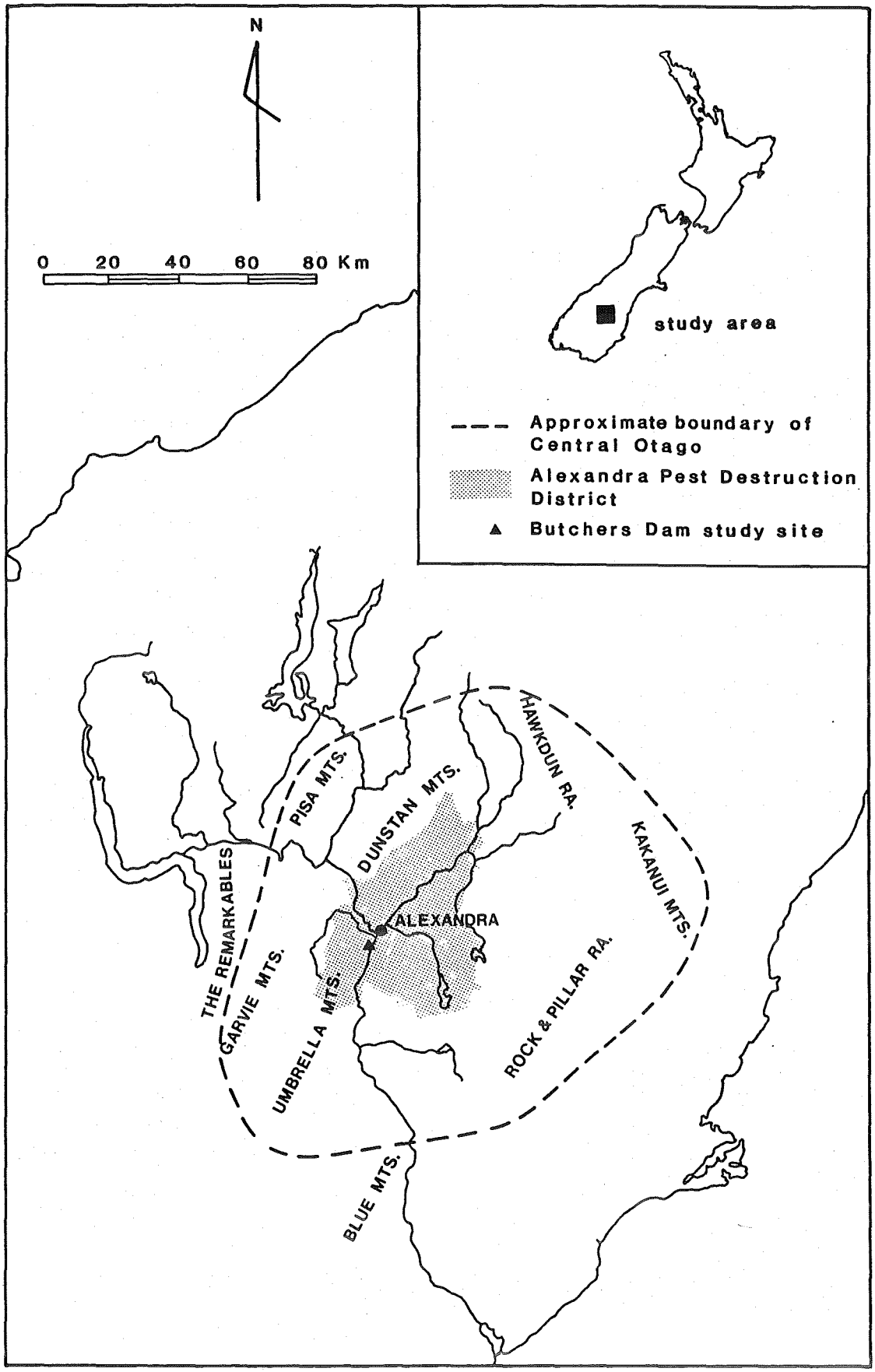


Figure 2.1 Map of Central Otago showing the Alexandra Pest Destruction District and the location of the Butchers Dam research area.

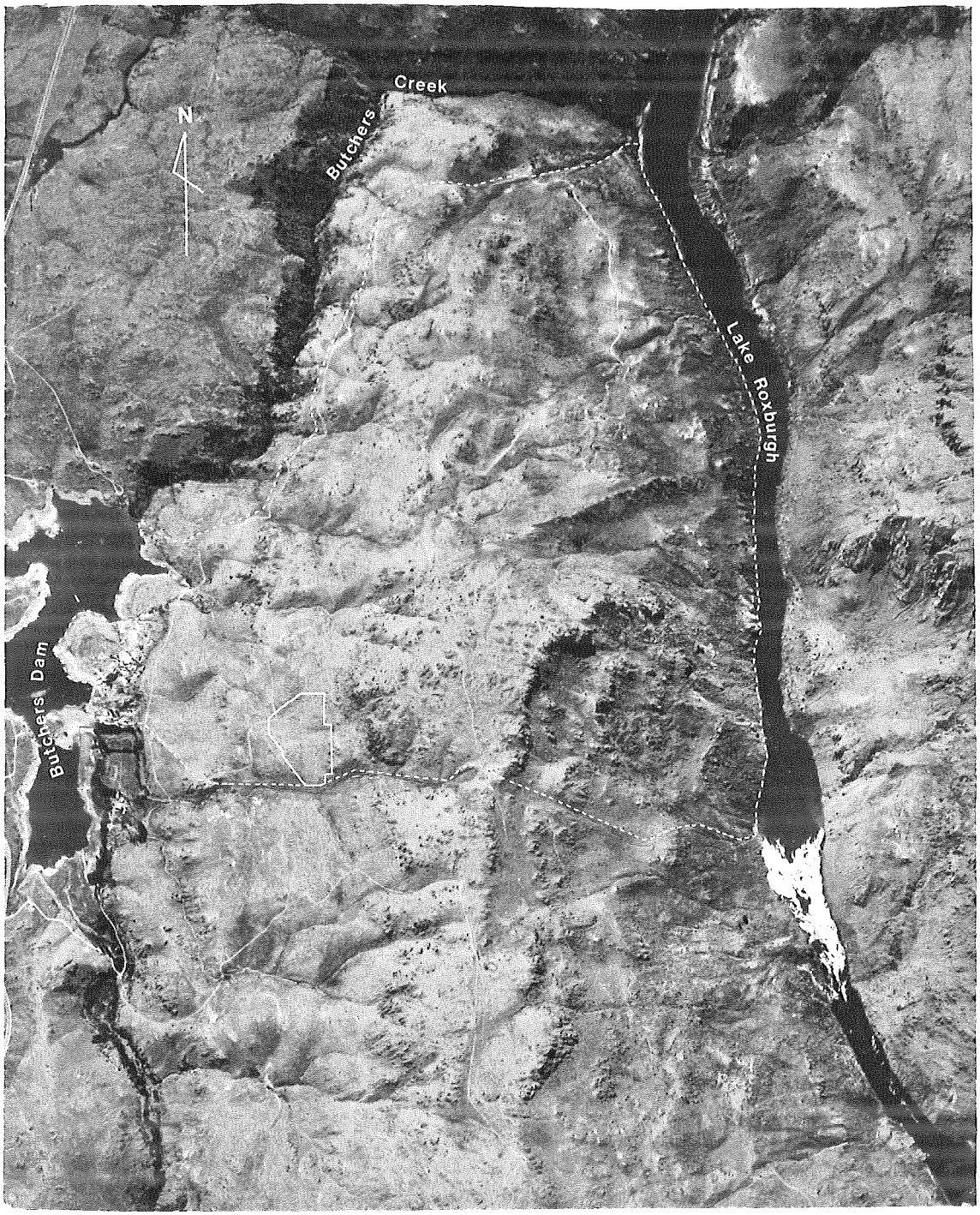


Figure 2.2 Aerial photograph of the Butchers Dam research area (dashed line) showing the location of the behaviour study site (solid line).

The landscape of the higher country has a rough, craggy appearance with numerous shallow valleys and low ridges. Outcrops of schist are common over the whole area, and the valley floors are generally marked by numerous shallow and ill-defined old stream channels and terrace scarps. The predominantly brown-grey earth soils are shallow and stony, except near the river banks where there are accumulations of loess (McCraw 1965).

On the western side the Butchers Dam study area rises from an elevation of about 250 m a.s.l. through a series of terraces and moderate slopes, to a main ridge running roughly north to south at an elevation of about 500 m. From this ridge it drops rapidly through several smaller terraces and steep rocky faces to the shore of Lake Roxburgh at 150 m a.s.l. The main ridge flattens out to a plateau of several hectares at its southern end. The north-western part of the area is characterised by a series of short, steep gullies and ridges.

The brown-grey earth soils are shallow over most of the area. Erosion has removed most of the soil to expose the parent schist, especially on the steeper slopes. The sloping land has a fretted appearance caused by numerous outcrops of steeply-dipping schist. Where the schist is flat-lying a tor landscape is present. Tors are pillars of schist, usually several metres high, which rise from relatively flat surfaces of bedrock covered with a shallow layer of soil. This landscape is common at the highest elevations of the area, especially over the southern plateau.

The site chosen for the behaviour investigations was one of the western terraces, with a relatively flat area of approximately 2 ha (Figure 2.3). This terrace was surrounded on three sides by moderate slopes which added another 2 ha to the observable area. The rabbit population was denser than on many other parts of the Butchers Dam block, because of the sunny aspect and good vegetation cover relative to much of the surrounding area.

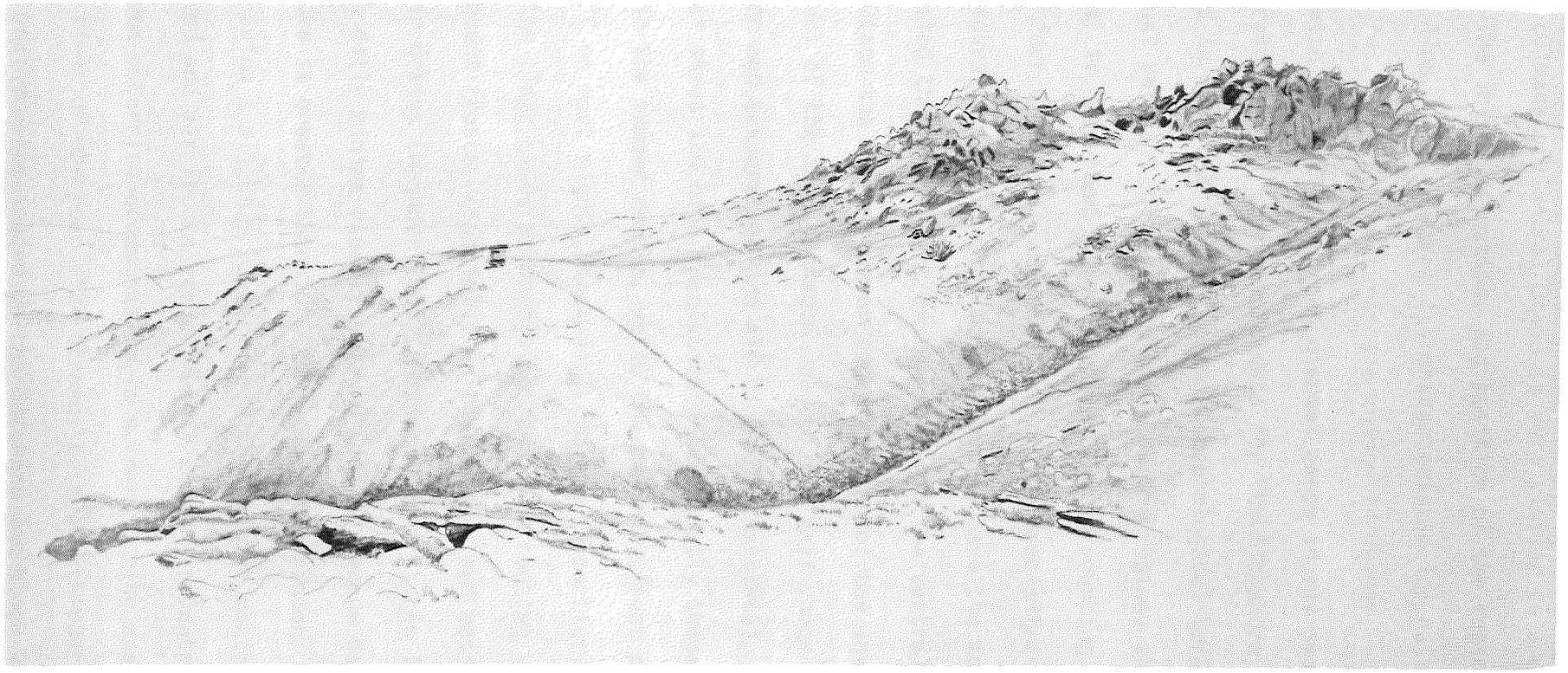


Figure 2.3 Artist's impression of the Butchers Dam study area showing the fence line and observation hut (near centre of picture).

2.3 Climate

The climate of Central Otago is very similar to a continental-type climate. The inland situation, and position of the region relative to the Southern Alps, give the area its characteristic low rainfall and extremes of temperatures. High temperatures are common in summer, very low temperatures in winter, with a relatively broad diurnal range in all seasons. Long-term mean monthly rainfall and temperature data for the Alexandra weather station are presented in Figure 2.4 (New Zealand Meteorological Service 1983).

Annual rainfall in the 'dry core' of the region, the area around Alexandra, is less than 350 mm although the surrounding ranges often receive three or four times this amount. Much of the precipitation at altitudes over 1000 m occurs as snow. Summer months usually have the most rainfall with winter being the driest part of the year. In the central valleys and basins of Central Otago the marked summer concentration of the low rainfall accentuates the dryness of the area, because most of the rain comes when temperature, insolation and evaporation are all high (Maunder 1965).

Clear skies and high insolation produce daily temperature maxima of 20°C or more in the summer months, while the reverse effect produces temperatures below 11°C on most nights. Nocturnal cooling is particularly important in winter, the clear skies and outgoing radiation causing very low temperatures with frequent frosts, especially in the valleys and basins into which the cooler air drains (Maunder 1965). Maximum temperatures in winter rarely exceed 10°C with daily minima usually below 0°C. The average daily range of temperature is greater than 10°C throughout the region, with summer months usually having a slightly larger range than winter months.

Ground and air frosts are extremely common in Central Otago, with ground frosts even occurring occasionally in summer. Spring and summer are the windiest times of the year with strong, gusty north-westerlies prevailing.

The weather experienced on the Butchers Dam block was typical of the dry core of Central Otago. The monthly means of the daily minimum and maximum

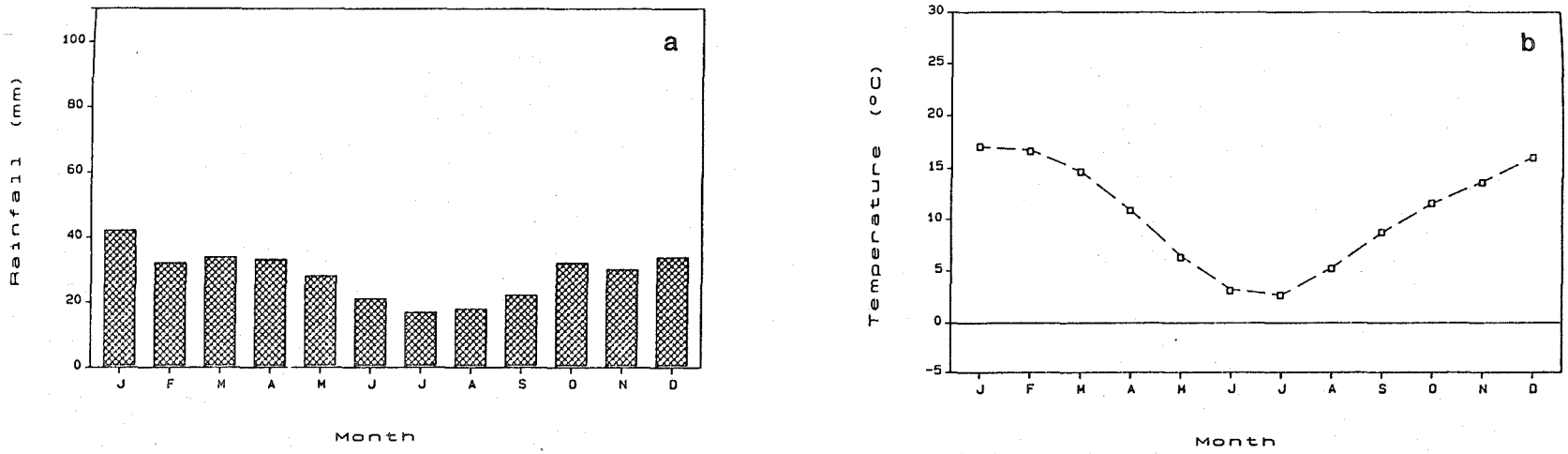


Figure 2.4 Long-term (a) mean monthly rainfall (1922–1980) and (b) temperature (1929–1980) observations for the Alexandra weather station.

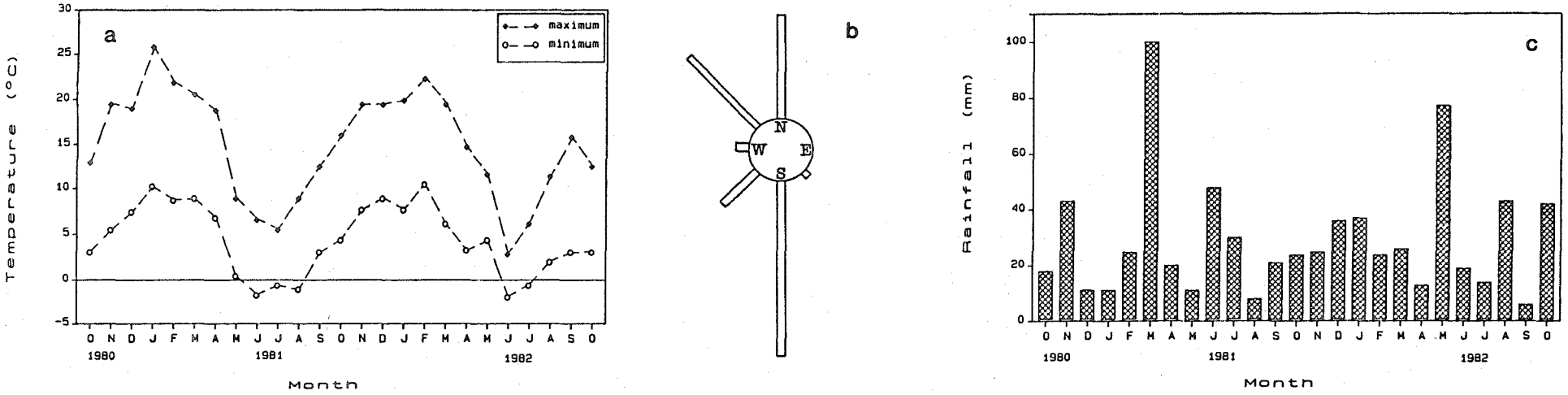


Figure 2.5 (a) Monthly means of daily minimum and maximum temperatures and (b) wind direction information recorded at Butchers Dam, and (c) monthly rainfall totals for the Earnscleugh weather station.

temperatures recorded on the study area together with monthly rainfall totals for the Earnscleugh climate station (New Zealand Meteorological Service 1980, 1981, 1982) less than 2 km away, are presented in Figure 2.5. Temperatures were often above 20°C on summer days, with the highest temperature recorded being 31.5°C in January 1981. In contrast, minimum temperatures in winter were usually below 0°C, with daily maxima rarely exceeding 10°C at this time of year.

Although the study area was sheltered from easterly winds, it received the full force of winds from the north, west and south. Prevailing winds were from the north and northwest, and from the south (see Figure 2.5), with spring and autumn being the windiest times of year. On windless days the sunny aspect of the terrace produced very warm conditions, even on winter days providing cloud cover was minimal.

Rainfall was less than 50 mm for all months except March 1981 (100 mm) and May 1982 (77 mm), with a trend towards slightly more rain in the summer months. Most precipitation was associated with cold, southerly winds. Sleet and snow fell several times during the course of the study.

Hoar frosts were not uncommon, the severest being in June 1982. In this case the temperature did not rise above -2°C for several days, and most objects were covered with a thick layer of frost (Figure 2.6).

2.3 Vegetation

Although there are eight major vegetation types in Central Otago (Mark 1965), much of the area is dominated by only two of these. Tussock (**Festuca** spp. and **Poa** spp.) grasslands occupy most of the hilly country between 500 m and 800 m, with the exact species composition dependent on slope and drainage characteristics, as well as altitude. Speargrass **Aciphylla aurea** is the only other common species on the hill country.

The second widespread vegetation type is a semidesert association characterised by low, dense cushions of scabweed **Raoulia australis**, and

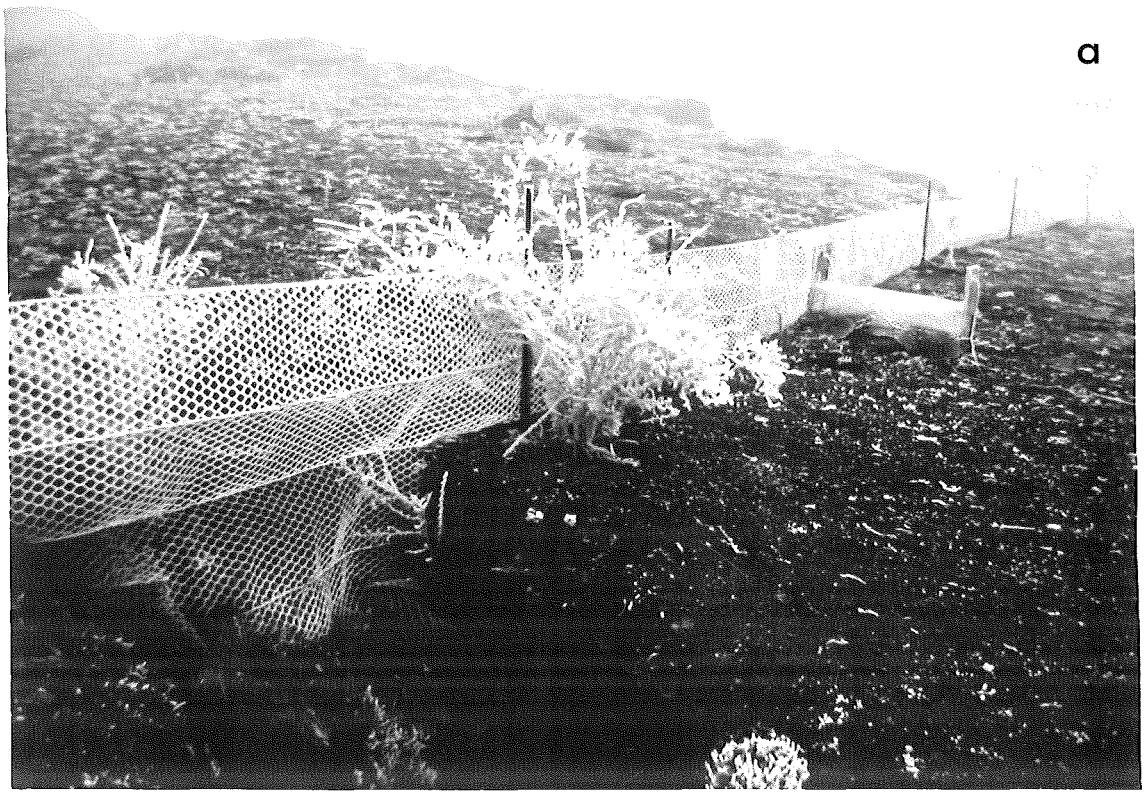


Figure 2.6 (a and b) Effects of a hoar frost on the Butchers Dam study area, June 1982.

occupies the driest parts of the region. Areas between the cushions of scabweed are often bare or occupied by small native and exotic grasses and weeds (Mark 1965). Some tussocks and matagouri **Discaria toumatou** are usually present in the gullies and damp hollows. This vegetation type is usually found on the foothills at lower altitudes than the tussock grasslands.

Pastoral farming has altered the vegetation associations especially on the foothills and valley floors, where introduced grasses now predominate, often under a regime of topdressing and irrigation. From last century the tussock-covered hills have been subject to frequent cycles of burning and heavy grazing pressure by sheep. Together with the effects of large numbers of rabbits, this regime has depleted the cover of tussocks in some areas, caused severe soil erosion, and allowed the spread of scabweed to higher altitudes (Mark 1965). High winds, common during the summer months, often accelerate the erosion.

On the Butchers Dam block the shallow soils, semi-arid continental-type climate, and heavy grazing pressure by rabbits have combined to produce a vegetation association that Mark (1965) terms semidesert. This association is common on slopes exposed to the north and northwest in the driest parts of Central Otago.

Cushions of scabweed cover much of the study area. Stonecrop **Sedum acre** is dominant over the northeast part of the area. Thyme **Thymus vulgaris** is commonest where the soil is shallow, especially on the moister, south-facing slopes. Several other species, including briar **Rosa rubiginosa** and speargrass, occur frequently on the slopes particularly next to large rocks where rainfall runoff drains. Hard tussock **Festuca novae-zelandiae** and matagouri are also found on the slopes. At least two species of lichen, as well as moss, most probably **Rhacomitrium languinosum** var **primosum** (B Wills pers. comm.), are dominant on the lowest part of the area where soil moisture content is relatively high. Californian thistle **Cirsium arvense** and scotch thistle **C. vulgare** are also common on this part of the area at certain

times of the year.

Many other plant species are numerous in the area but generally during the spring and summer months only. These are the annuals and include bidi bidi **Acaena novae-zelandiae**, annual mouse-eared chickweed **Cerastium glomeratum**, horehound **Marrubrium vulgare**, moth mullein **Verbascum virgatum**, vipers bugloss **Echium vulgare**, haresfoot trefoil **Trifolium arvense**, scarlet pimpernel **Anagallis arvensis**, Californian poppy **Eschscholtzia californica**, St Johns wort **Hypericum perforatum**, forget-me-not **Myosotis caupitosa**, sorrel **Rumex acetosella**, and storksbill **Erodium circutarium**. Although succulent daisy **Vittidinia australis** was widespread in the spring and early summer of 1980, it was rare the following year. A significant proportion of the area is patches of bare earth, both on the slopes and the flatter parts. Mark (1965) aptly labelled these patches erosion pavement.

3 GENERAL METHODS

3.1 Fieldwork timetable

Actual field work and collection of behaviour data began in October 1980 and concluded in October 1982. Field trips were monthly and usually lasted 10-14 days. Prior to this, between June and September 1980, several field trips were required to establish the experimental set-up outlined below. Collection of autopsy material continued to January 1883, with isolated samples obtained in March and July 1983 also.

3.2 Behaviour studies

An observation hut was established on the study site, following modifications to include two large double-glazed windows. These windows made observations over a wide area possible from a single position, while double-glazing reduced problems with condensation. The field of view was increased by raising the hut approximately 2 m above the ground on a support framework of railway sleepers (Figure 3.1).

The study site was marked out with a 15 x 15 m grid system. Wooden pegs with numbers or letters attached marked the corners of each grid square. Fluorescent paint was applied to the pegs so they were easily seen and locations could be quickly determined. This meant that the positions of all behaviour observations could be accurately recorded.

3.2.1 Trapping and marking

An important prerequisite of the study was the establishment of a live-catching system so that rabbits could be marked and basic biological information recorded. Two factors restricted the usefulness of traditional capture techniques. Firstly, the majority of rabbits had their usual resting places high in the rocky outcrops bordering the eastern edge of the study area (see Figure 2.3). Preliminary observations revealed that only during the main

Figure 3.1 Hut used for behaviour observations.

Figure 3.2 Smeuse trap with captured rabbit (note the tag in the right ear).

daily activity period did most rabbits venture down onto the gridded, observable area. Secondly, the use of baited traps was precluded by the need to test the hypothesis of neophobic behaviour towards poison baits later in the study.

Knowledge of the daily movement patterns of the rabbits was used to devise a successful trapping procedure. A fence approximately 1 m high was constructed around the central, flattest portion of the observable area (approx. 2 ha) using rabbit-proof netting. Preliminary observations had revealed that the majority of rabbits fed within this area. Thirty-four smeuse traps were located at almost regular intervals along the 585 m fence line. These traps were also constructed from rabbit-proof netting with a frame of steel rod at each end, and transparent doors of polycarbonate hinged on these frames (Figure 3.2). Similar types of smeuse traps have been used previously by Southern (1940), Dunnet (1957b), and Mykytowycz (1958). Rabbits could gain access to the preferred, enclosed area only by using the smeuse traps.

It was necessary to proceed slowly during the construction of the fence and locating of the traps in order to minimise disturbance to the population and to avert any changes in their daily movement patterns. Work advanced in stages, 3 to 6 weeks apart, during which time it was hoped that rabbits would become accustomed to the changes in their environment. The various stages were:

1 Construction of the fence with the netting doubled up to give access along the entire fence line.
2 Netting lowered and lined with rocks to prevent rabbits digging beneath the fence, and holes cut where traps were to be sited, allowing movement to and from the enclosed area.
3 Smeuse traps (with both doors tied up) located at each of the thirty-four holes along the fence line.
4 Inner doors lowered.
5 Outer doors lowered.

During the final two stages the rabbits had to 'learn' to push the doors open with their noses in order to enter or leave the fenced area.

The smeuse traps were set by placing two steel pins diagonally across the outer lower corners of the doors (see Figure 3.2). Consequently the doors opened inwards but not outwards, capturing any rabbit moving in or out of the area. The regime of trap setting varied considerably over the duration of the study. Traps were checked immediately after sunrise and again following the completion of behaviour observations each day, normally 60–90 minutes after sunset.

Early in the study (November and December 1980) a small number of rabbits were captured by digging out burrows, either on the study site itself or from nearby areas. This procedure was very time consuming and caused a large amount of disturbance, so was abandoned in favour of smeuse trapping only. Captured rabbits were sexed, weighed, examined for reproductive status, and marked with individually colour-coded ear tags. These tags were constructed from 2 cm lengths of plastic tubing (8 mm in diameter) and bore up to 3 bands of coloured reflective tape. The tag was attached to the ear with a loop of stainless steel wire. The attachment site was normally on the lower margin near the base of the ear where strong ridges of cartilage reduced the possibility of tag loss (if snagged on vegetation or during grooming, fighting, etc.). Male rabbits were tagged in the right ear, females in the left ear, for ease of identification. In addition, a much smaller, numbered Monel tag was placed in the upper margin of the opposite ear in case of main tag loss.

3.2.2 Behaviour observations

Observations took place on a number of days each month, usually beginning in the early afternoon and continuing to about one hour after sunset. Preliminary observations and previous studies (e.g. Dunnet 1957b, Rowley 1957b, Gibb et al. 1978) had revealed that this was the period when rabbits

were most active. All observations were made using either Pentax 8x40 binoculars or a Kowa telescope with a 67 mm objective lens and a 20-60x eyepiece. These visual aids made observations of the rabbits' activities easier and enabled accurate reading of tags at distances up to about 100 m. Some observations during the early hours of darkness were made using a Zeniscope NVC-100 night vision system. Images seen through the Zeniscope are monochromatic, so identification of tagged individuals was not possible. The difficulty of moving and continually focussing the Zeniscope restricted its use to focal sampling only (see below). Frequently, a marked rabbit would be identified close to sunset and then several successive focal animal samples performed. Observations were recorded either directly onto data sheets or stored on a foot-operated tape recorder for subsequent transcription.

A quantitative approach was employed for the collection of most behavioural data, using a repertoire of 53 discrete behaviours, similar to that employed by Australian workers in previous studies. Important considerations were that individual behaviours should be repeatably recognisable, relatively homogeneous, and that the total number of behaviours was manageable. The 53 behaviours recognised fell into 10 distinct categories (Table 3.1). A brief description of each behaviour is given in Appendix 1. Transect sampling and focal animal sampling were the main observation methods used and are outlined below.

Transect sampling

Regular sweeps of the study area were made following the grid pattern, noting the location, activity, and identity (if tagged) of all rabbits encountered. Each activity recorded during transect sampling was based on an observation lasting approximately 5 seconds. If the rabbit was in a state of transition from one behaviour to another, the latter was recorded. However, if the behaviour involved was one of the very fleeting ones lasting only one or two seconds (e.g. enurination), the 5-second criterion was not applied.

Table 3.1 Categories used for classification of rabbit behaviour.

MISCELLANEOUS	LOCOMOTORY	TERRITORIAL
1 entering burrow	28 lope	46 tail-flagging
2 emerging from burrow	29 run	53 chinning
3 looking down burrow	30 skit	54 patrolling
4 digging burrow		
5 defecating	ALERT	AGGRESSIVE
6 urinating	31 upright	55 threat
FEEDING	32 crouch	56 move away
	33 thump	57 chase
7 grazing	34 fleeing	58 chased
8 browsing		61 fighting
9 scratch feeding	REPRODUCTIVE	
11 coprophagy		DISPLACEMENT
	36 inspects	
GROOMING	37 inspected	62 scraping
	38 following	63 paw-shake
15 scratching	39 followed	64 hayraking
16 washing	40 circling	65 challenging
17 shaking	41 circled	
18 mutual grooming	42 enurinates	
24 stretching	43 enurinated	
25 yawning	44 nuzzles	
26 rolling	45 nuzzled	
	47 copulation attempt	
RESTING	48 mounted	
	49 copulates	
20 sitting		
21 squatting		
22 lying		
23 basking		

Focal animal sampling

This consisted of continuous observation of one individual for 10 minutes. A complete record of its behaviour was made, including any interactions with other individuals. The rabbit's identity and location were recorded as well as the duration of each behaviour. This method was particularly well suited to gathering information on sex, age, and social status classes within the population. Therefore, an effort was made to concentrate on marked individuals only, and to collect information from as

many different individuals as possible. Occasionally, it was possible to perform focal sampling on two rabbits simultaneously as long as activity patterns remained simple.

Both these methods have advantages and disadvantages. Transect sampling does not provide information on specific behaviour durations or sequences, whereas focal sampling is often biased towards those individuals most easily seen. Also, when concentrating on one individual it is easy to miss events occurring nearby that may influence the behaviour of the focal animal. Nevertheless, the information available from these two sampling techniques is complementary and overall should present an accurate account of the rabbit's activity.

Transect sampling was carried out from October 1980 to October 1982 inclusive, and focal sampling from February 1981 to October 1982 inclusive. For some forms of behaviour (e.g. reproductive and aggressive) it was not possible to collect enough information from quantitative sampling alone. In these cases it was necessary to record information when a particular situation arose, regardless of time. Such non-quantitative data were especially useful in supplementing information on group social structure and reproductive interactions.

Regular records of weather conditions were made during the course of behaviour sampling. Parameters noted were temperature, cloud cover, wind direction, wind speed, as well as precipitation, if any. The presence of predators, mainly harrier hawks **Circus approximans** and feral cats, was also noted.

3.2.3 Vegetation survey

Twenty-four representative sites within the observed area were chosen for vegetation analysis using the stereoscopic plot technique. Sites were chosen because they characterised the major vegetation associations on the area.

Pairs of colour slides were taken using an Olympus OM-2N 35 mm camera with a wide angle lens and Agfa 50S film. The camera was mounted on a moveable tripod with two camera positions. One slide was taken at each position. Vegetation slides were taken first in June 1981, and then in July 1981 and at three month intervals subsequently.

In the laboratory the pairs of slides were projected onto a transparent table to give a stereoscopic image, on which was superimposed a grid of 100 random points. Each point was scored according to the plant species present or whether the point fell on bare earth or rabbit faeces. Nineteen plant species were recognised, with those that could not be determined being placed in an 'unidentified' category. A distinction was made between live and dead vegetation. Each series of slides for a particular plot were aligned exactly, so that the same 100 points were examined. In this way an accurate assessment of the changes in the vegetation cover on the area could be made.

3.3 Neophobia experiments

Three experiments were conducted during the course of the study to investigate neophobic behaviour.

1 Firstly, a preliminary exercise designed to test procedures for the main poisoning experiment was conducted on a small area of farmland, known as the 12-mile block, less than 1 km from the main study site at Butchers Dam. This area has a history of regular rabbit control operations.

2 The second experiment was the poisoning of the study population at Butchers Dam.

3 Finally, an experiment designed to test the constancy of behaviour patterns displayed by individuals during the poison operation was conducted on the survivors from the Butchers Dam population. In this case, golf balls were used as the foreign object in the rabbits' environment.

3.3.1 The 12-mile block poison trial

A canvas hide was erected on a rocky outcrop overlooking a small terrace of about 1 ha. Two strips of quadrats (5 x 5 m) were marked out in the centre of the area, using wooden pegs coloured with fluorescent paint. These pegs were used as reference points when recording the position of rabbits and, during the poisoning, as a guideline for laying the furrow and baits (Figure 3.3).

Observations took place on 11 days between June and September 1981. June and July observations covered the pre-poisoning phase, the poison trial was carried out in August, and post-poisoning observations were made in September. Regular scans of the whole terrace area were made, similar to transect sampling, recording the position and activity of all rabbits seen. No effort was made to catch and individually mark rabbits in this population. However, some individuals did have distinguishing fur markings so that identification of a few rabbits was possible. Each scan sample also provided a count of the total number of rabbits present at that time. As with behaviour observations on the main study area, an effort was made to collect most data during the late afternoon, when the greatest number of rabbits were active.

Following the observations on rabbit numbers and behaviour over the preceding two months, a small-scale poison operation was carried out in August 1981 using 1080 poison on carrot baits. The standard procedure employed by Pest Boards of two applications of non-toxic carrot baits followed by the toxic bait was used. Non-toxic baits were dyed with Rhodamine B (0.05% w/w) which stains the mouthparts of rabbits consuming baits and can be detected with an ultra violet light for several weeks after consumption (Bell 1973). By this means rabbits killed by toxic baits could be checked to determine if they had previously consumed non-toxic baits. Toxic baits had 1080 applied at a rate of 0.02% w/w. In addition, the toxic baits were dyed green with Lissamine B to minimise bait acceptance by birds (Caithness and Williams 1971). Baits were laid in and around a hand-drawn furrow which bisected the parallel series

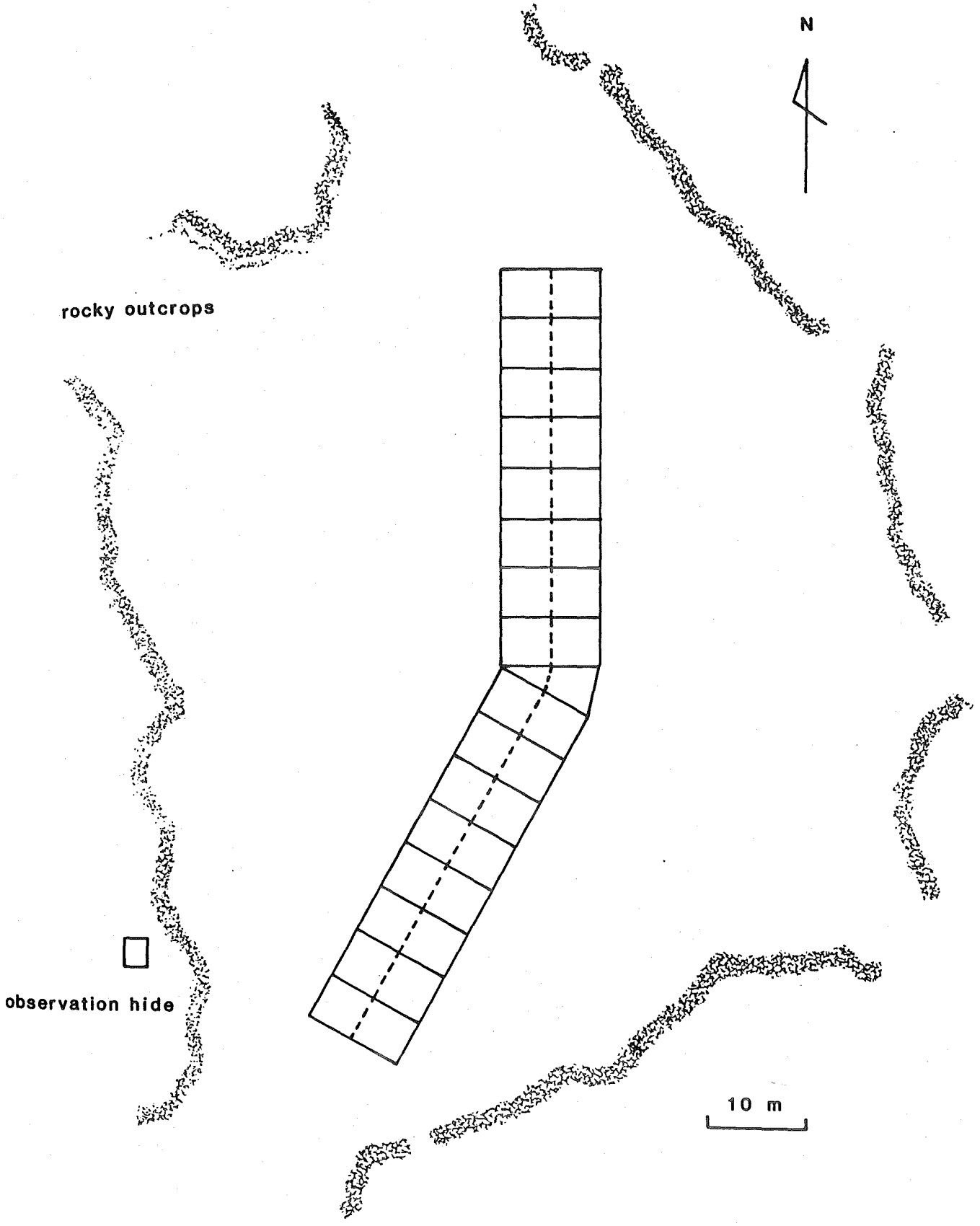


Figure 3.3 Lay-out of the 12-mile block poison trial area showing the quadrats and the position of the furrow and baits (dotted line).

of quadrats (see Figure 3.3).

Scan sampling continued during the afternoon activity periods on most days for the duration of the control operation. Daily counts were made of the number of baits remaining in each 5 m section of the furrow, during both the pre-feed and poisoning phases of the trial. Rabbits found dead on the area were frozen for subsequent autopsy after an eye lens had been removed for ageing purposes.

3.3.2 Butchers Dam poison experiment

This experiment was carried out in August 1982. As with the 12-mile block poison trial, this control operation followed the normal Pest Board procedure of two applications of non-toxic bait followed by the application of toxic bait. Carrot baits were produced using a Reliance bait cutter and screened with a Reliance rotary bait screen. Although this screen removes up to 40% of the chaff, the remaining baits were sieved by hand to ensure that only baits above approximately 1 g were included. Non-toxic baits were dyed with Rhodamine B and toxic baits with Lissamine B, as in the preliminary trial. The 1080 poison was applied to the baits at a rate of 0.04% w/w.

A furrow approximately 500 m long was drawn through the area inside the fenceline (Figure 3.4). The course of the furrow was chosen to pass through as many of the rabbits' activity ranges as possible. Baits were laid by hand, at a rate of approximately 12.5 kg per ha, along the entire furrow except where it passed through five pre-selected grids. In these grids the furrow was left unbaited. Two bait lines without a furrow, each 40 m long, were laid between sections of baited furrow. Two shorter bait lines were also laid, one (15 m) inside and one (20 m) outside the fenceline. Unlike the longer bait lines, these two were not continuous with any baited or unbaited furrow (see Figure 3.4).

The rate of bait disappearance was monitored by daily bait counts, throughout all stages of the operation, in each of 14 regularly spaced 5 m

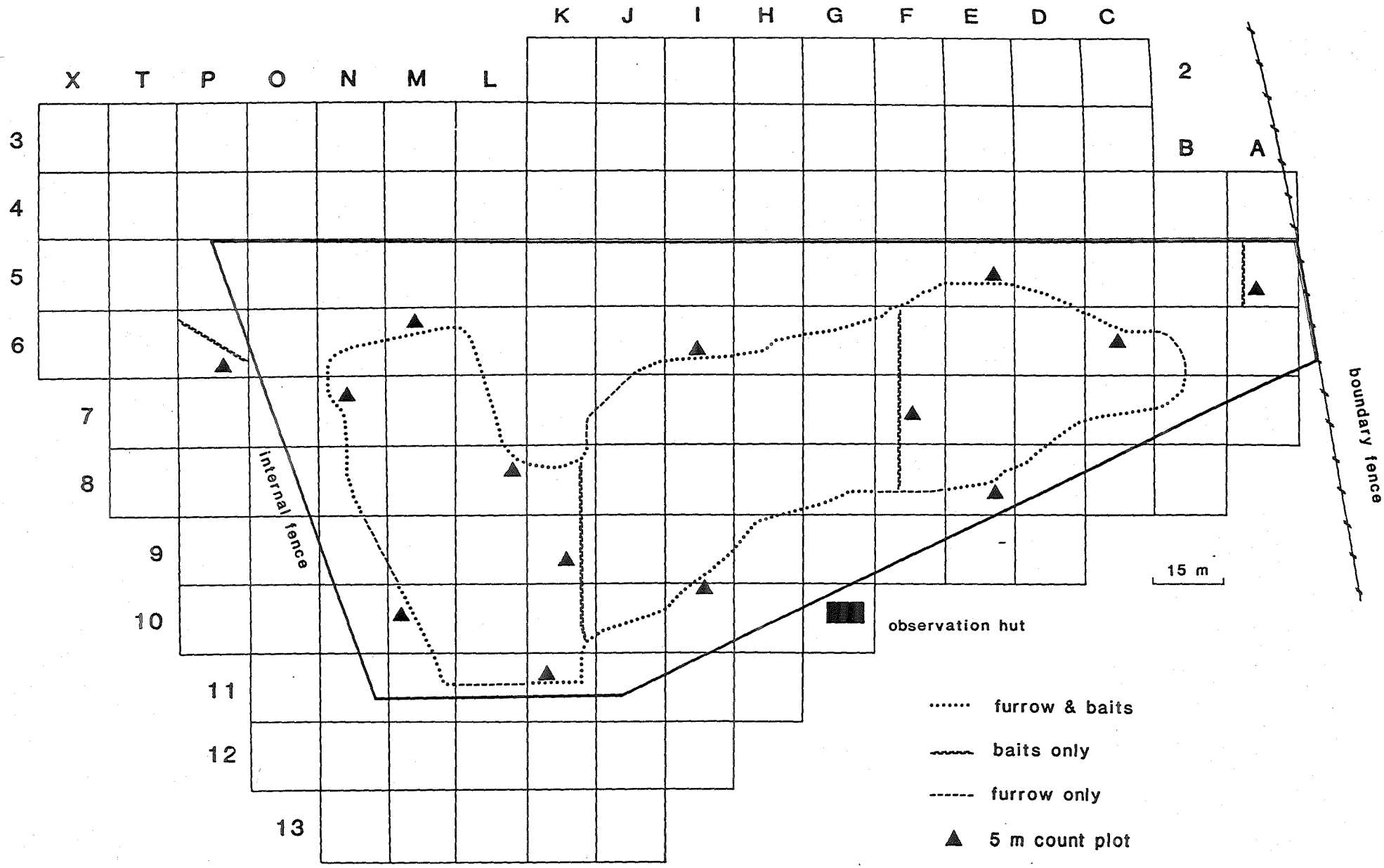


Figure 3.4 Butchers Dam study area showing the lay-out of the poison operation.

plots. Before the second non-toxic bait application and the toxic bait application all remaining baits in these plots were removed. Some were partially eaten and others dehydrated and shrivelled after lying in the furrow for almost a week. They were unlikely to be attractive to rabbits and therefore including them in subsequent bait counts would bias the resulting bait disappearance estimates. Counts were usually made around mid-morning when disturbance to the population would be minimal. Following the poisoning, searches were made to collect as many carcasses as possible. This was done twice each day, first in the early morning and again about 2 hours after sunset, for one week following the application of the toxic bait.

3.3.3 Golf ball experiment

For two days during the October 1982 observations, three sets of golf balls were placed within the study area. Each set consisted of a line of 4 golf balls, placed 1 m apart, in a particular grid square. The grids were chosen because they were much used by rabbits in the previous few days and changes in patterns of distribution and behaviour would be easy to notice. Normal transect and focal animal sampling continued while the golf balls were in place, although special effort was made to note the behaviour of rabbits in the vicinity of the golf balls and any changes in behaviour upon encountering them.

3.4 Autopsy samples

Samples of rabbits killed during normal Pest Board control operations were obtained each month. All samples came from areas within the Alexandra Pest Destruction Board district. These rabbits had either been shot, mostly at night using spotlights, or poisoned with 1080 on oat or carrot baits. An effort was made to obtain about 100 rabbits each month, although this was not always possible.

Rabbits were autopsied within 24 hours of death. Each rabbit was sexed, and its total length and weight recorded. Reproductive status was determined: in males the position of the testes was noted as either abdominal or scrotal; females were checked to see if they were pregnant or lactating. In the case of pregnant females, the number of embryos and resorption sites was counted; an embryo was then removed from the uterus and its age determined from an age-length curve (J M Williams unpub.).

A subjective index of abdominal fat was recorded using a scheme similar to that used by Riney (1955) for red deer **Cervus elaphus**. The amount of fat present in the dorsal and lateral region of the body cavity around the kidneys was scored on a scale of 0-3 as follows:

0 no trace of fat obvious in the region around the kidneys;

1 small amounts of fat present around the kidneys, but not extending anteriorly or posteriorly in the body cavity;

2 moderate amounts of fat present around the kidneys and extending several centimetres along the dorsal and lateral surfaces of the body cavity, anterior and posterior to the kidneys;

3 large amounts of fat surrounding the kidneys, almost obscuring them, and extending in thick bands onto the stomach anteriorly and the small intestine posteriorly.

One eyeball was removed intact from its socket and placed in a vial of 10% formalin for subsequent ageing using the technique originally devised by Lord (1959) for cottontails **Sylvilagus floridanus** and subsequently developed for European rabbits by Myers and Gilbert (1968).

From July 1981 onwards a number of internal organs were also removed and stored in 10% formalin for later examination and measurement. The liver, kidneys and their associated fat, adrenals, and ovaries or testes were taken, and the left and right organs stored in separate containers.

In the laboratory perirenal fat was removed using the technique described by Riney (1955). Cuts were made tangential to the anterior and posterior ends

of the kidney and the remaining fat and tunica fibrosa were peeled away from the kidney. All material was weighed on a Mettler PC 440 pan balance. Liver weight was recorded to the nearest 0.1 g, kidney, perirenal fat, and testis to 0.01 g, and ovary and adrenals to 0.001 g. Each ovary was cut with a scalpel into approximately 1 mm sections so that the number of corpora lutea could be counted macroscopically.

4 INTRODUCTION TO THE BEHAVIOUR SECTION

Among the lagomorphs, the behaviour of the European rabbit is the most widely studied, especially since ecologists have recognised that behaviour is an integral part of a population study. The considerable volume of information on the rabbit probably reflects the widespread distribution and economic importance of this species. As early as the 1940s Southern (1940, 1948) included information on behaviour in his studies on the ecology and population dynamics of a natural population of wild rabbits in England. Southern (1940) was the first to outline the main behavioural characteristics of the species, namely dominance hierarchies, territoriality, and the sedentary way of living. Subsequently, exhaustive studies of rabbit behaviour have been conducted in Great Britain and Australia with the aim of learning more about a species which had become a serious pest in these countries (e.g. Myers 1958, Myers and Poole 1959, 1961, 1963, Mykytowycz 1958-61, Lockley 1961).

A considerable number of studies on rabbit behaviour have either used domestic breeds of the species or concentrated on wild rabbits in captivity. The latter is especially true of much of the early Australian work. However, recently a shift in emphasis towards behaviour studies of natural populations of lagomorphs has developed. This is mainly in response to the need for more efficient management of natural populations, not only where they are pests but also where conservation of particular species is desirable (Mykytowycz 1981).

The emergence of ethology, and more recently of sociobiology, as separate disciplines has added impetus to the study of lagomorphs, in particular the rabbit, which is a highly social species. The rabbit is an ideal subject in many ways for ethological studies: it is large enough to be watched with the aid of simple optical equipment; it can be relatively easily caught and marked; it is sedentary, gregarious, and not strictly nocturnal; and, it generally occupies habitats where vegetation cover does not hinder observation.

Within New Zealand only one previous study (Gibb et al. 1978) has dealt with aspects of rabbit behaviour. Their observations on daily activity mainly relate to how the rabbit's behaviour responded to increasing population pressure and a diminishing food supply. Because of the extent of the rabbit problem in parts of Central Otago and the continuing high costs of control, a more complete picture of the rabbit's behaviour was considered necessary if progress towards increasing the effectiveness of control measures was to be made. Unlike many of the previous studies, the present study was carried out in a region where the habitat and climatic conditions are relatively similar to those of the rabbit's Mediterranean homeland.

Emphasis was given to the collection of quantitative data, which were especially useful for comparisons with previous work done in Australia. The considerable data base also provided a 'standard' of behaviour, against which changes occurring during the control operation phase of the study could be compared.

Activity data collected during the course of the study were used to provide information on several aspects of behaviour which form the basis for the following chapters. These are:

5 Emergence

6 Activity budgets

7 Social organisation

8 Movement and activity range

9 Mark-recapture

Each of these chapters begins with a more detailed introduction to the aspect being investigated. As well as a brief review of the current knowledge on the topic, the main features examined are outlined.

5 EMERGENCE

5.1 Introduction

Most animals show circadian rhythms of activity. The control of these cyclic behaviour patterns is usually a result of complex interactions between exogenous environmental cues and endogenous physiological factors (Marler and Hamilton 1966). Previous studies of the onset and cessation of activity in mammals have demonstrated a strong relationship to changes in the level of light intensity (Bruce 1960, DeCoursey 1960, Mech et al. 1966, Lemnell and Lindlof 1981, Matuszewski 1981). Other exogenous factors are probably not as important but nevertheless act to produce variations on the main theme.

In rabbit populations the time of onset of activity or emergence period is highly variable, subject to both long-term (seasonal) and short-term (disturbance) variations (Rowley 1957b). Dunnet (1957b) reported that on some occasions all the members of a population had emerged before dusk, but it was more common for only 55-75% of the population to be active by this time. Southern (1948) found it was usual for only 30% of the population he studied to be on the surface at any one time.

The purpose of this chapter is to examine the emergence of rabbits in the study population, the features and variations it exhibits, and what factors appear to exert an influence on emergence.

5.2 Results

Throughout the study emergence followed a fairly similar pattern: rabbits began to appear in the early or mid-afternoon and numbers built up steadily to a peak which occurred at or slightly before sunset (Figure 5.1). Although a small number of rabbits could often be seen on the area earlier in the day, they were generally inactive. No sudden increases in the number of rabbits present were noted. However, small decreases between successive transect counts were not uncommon. The exact timing of emergence on different days

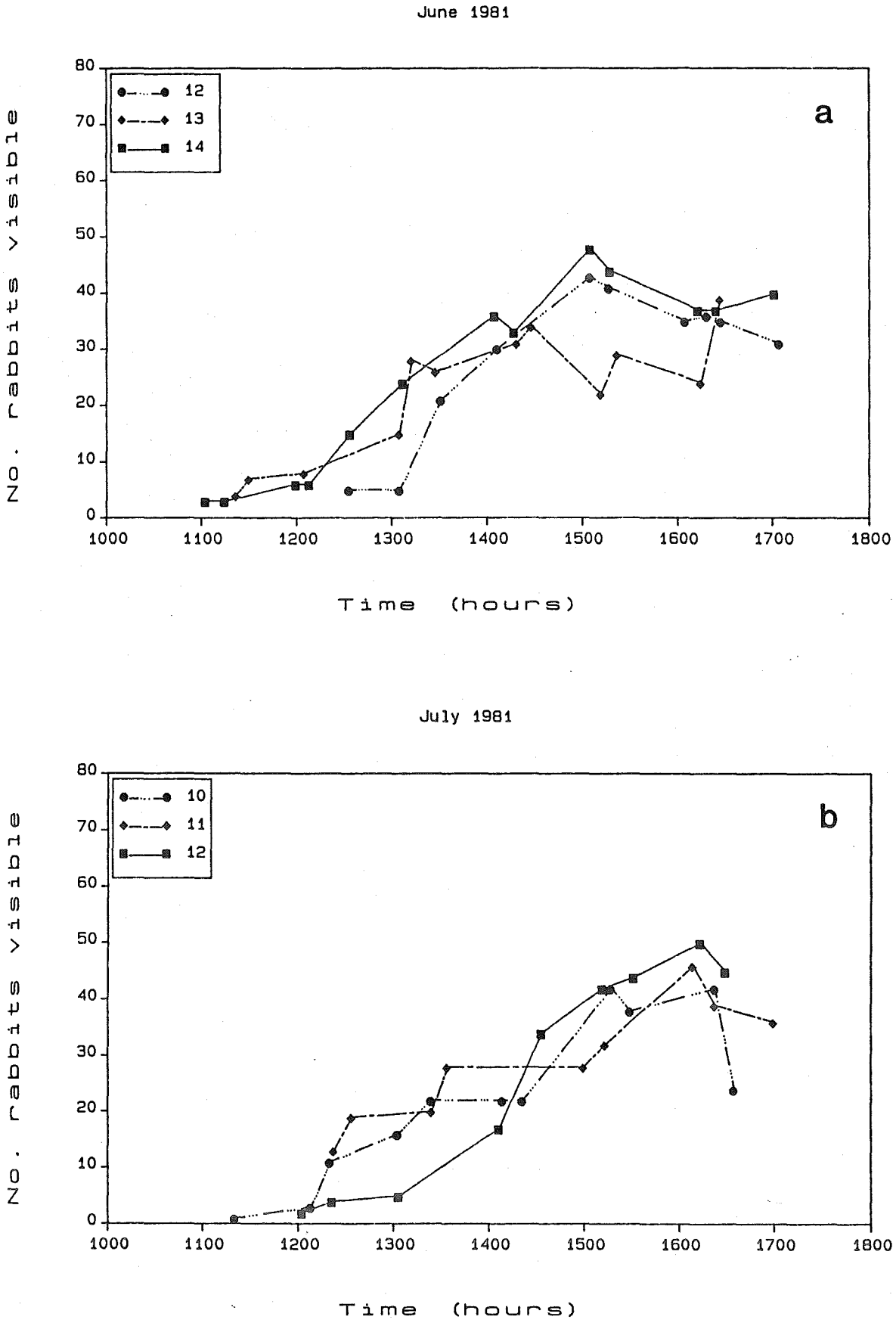
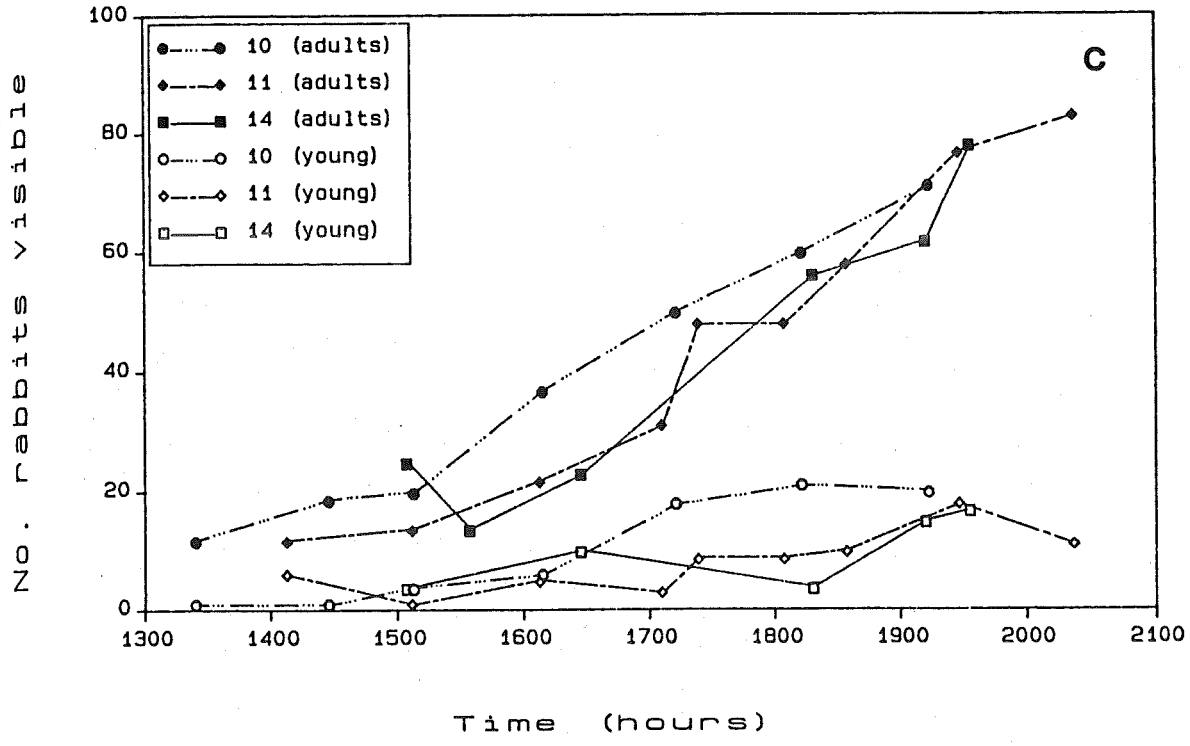
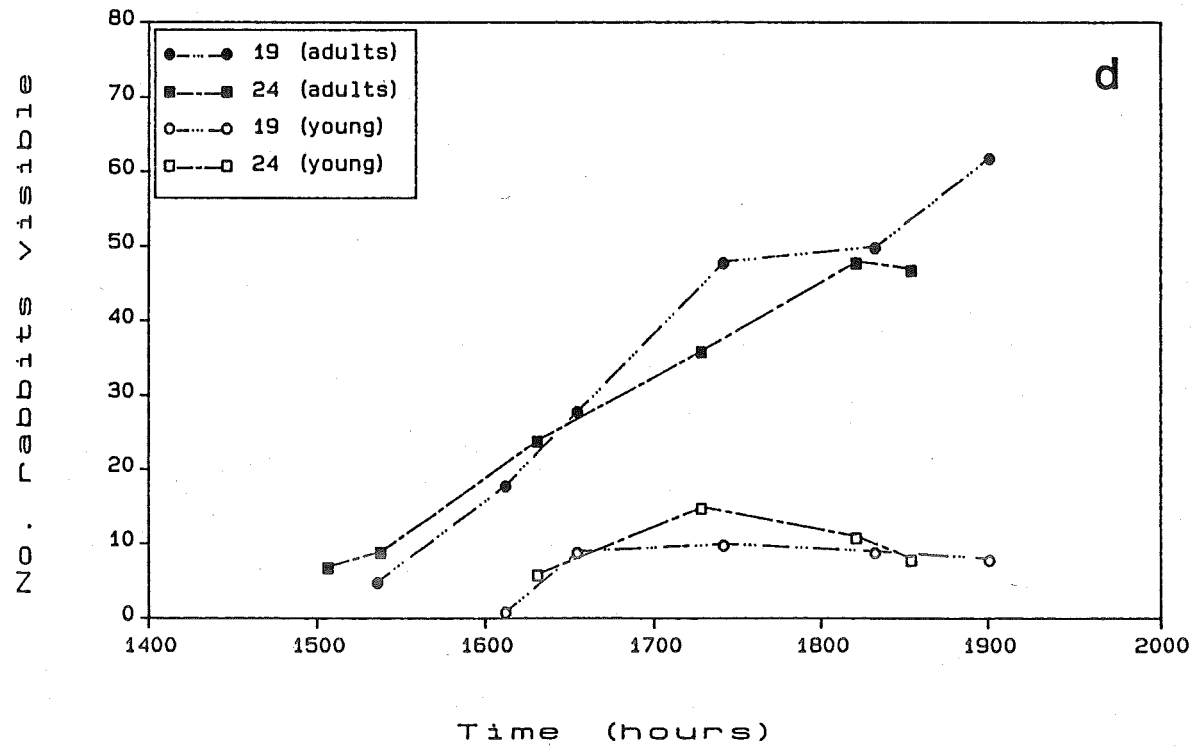


Figure 5.1 (a-f) Daily emergence patterns for young and adult rabbits on several days in each of six selected months.

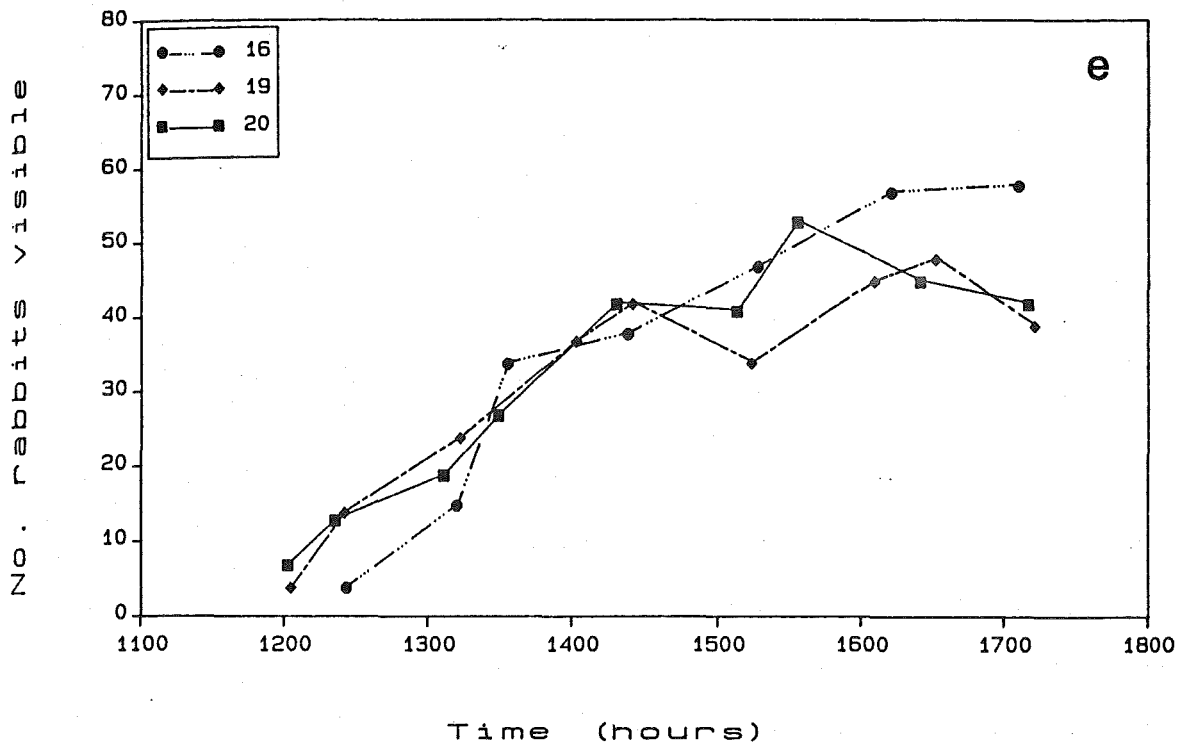
November 1981



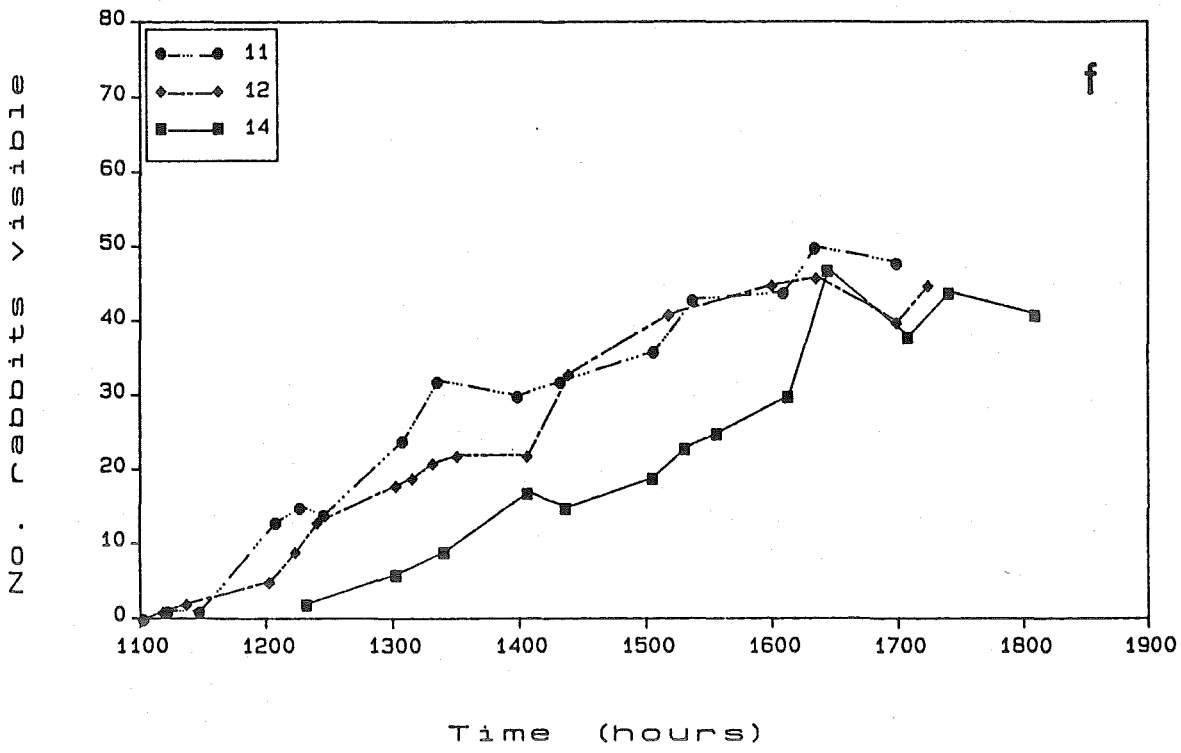
March 1982



July 1982



August 1982



within the same month was variable, although the rate of emergence was often remarkably similar.

Emergence of young rabbits was similar to that of adults, although they tended to become active slightly later and generally reached their maximum level of emergence earlier (see Figure 5.1). Young rabbits were more susceptible to disturbances, mainly from hawks, but sometimes most of the young would flee for cover for no obvious reason. These apparent false alarms were often associated with strong wind gusts. Consequently, erratic fluctuations between successive transect counts of the number of young present were common (Figure 5.2). The effects of these frequent and minor disturbances did not last long and usually most individuals reappeared soon afterwards. However, major disturbances such as human presence had prolonged effects and it was often more than 60 minutes before individuals began reappearing. Adults were also susceptible to these major disturbances.

The transect counts were pooled for each month and classified into 15-minute intervals. These results show that emergence occurred earlier in the winter months and later in the summer months, a seasonal fluctuation obviously related to day length (Figure 5.3). The initially high levels recorded for April, May, and December 1981 are due to slightly later start times for observations in these months and do not reflect a difference in emergence patterns. In general, activity began earlier in the second year of the study, especially during the spring and summer months. This earlier emergence was associated with a higher population density.

For comparative purposes three indicators of the population's level of emergence were examined. These were the time at which:

1 25% of the population were feeding,

2 50% of the population were emerged, and

3 the maximum number of rabbits were active.

These indicators show considerable variation within each month, although maximum emergence is less variable than the other two indicators (Figure 5.4).

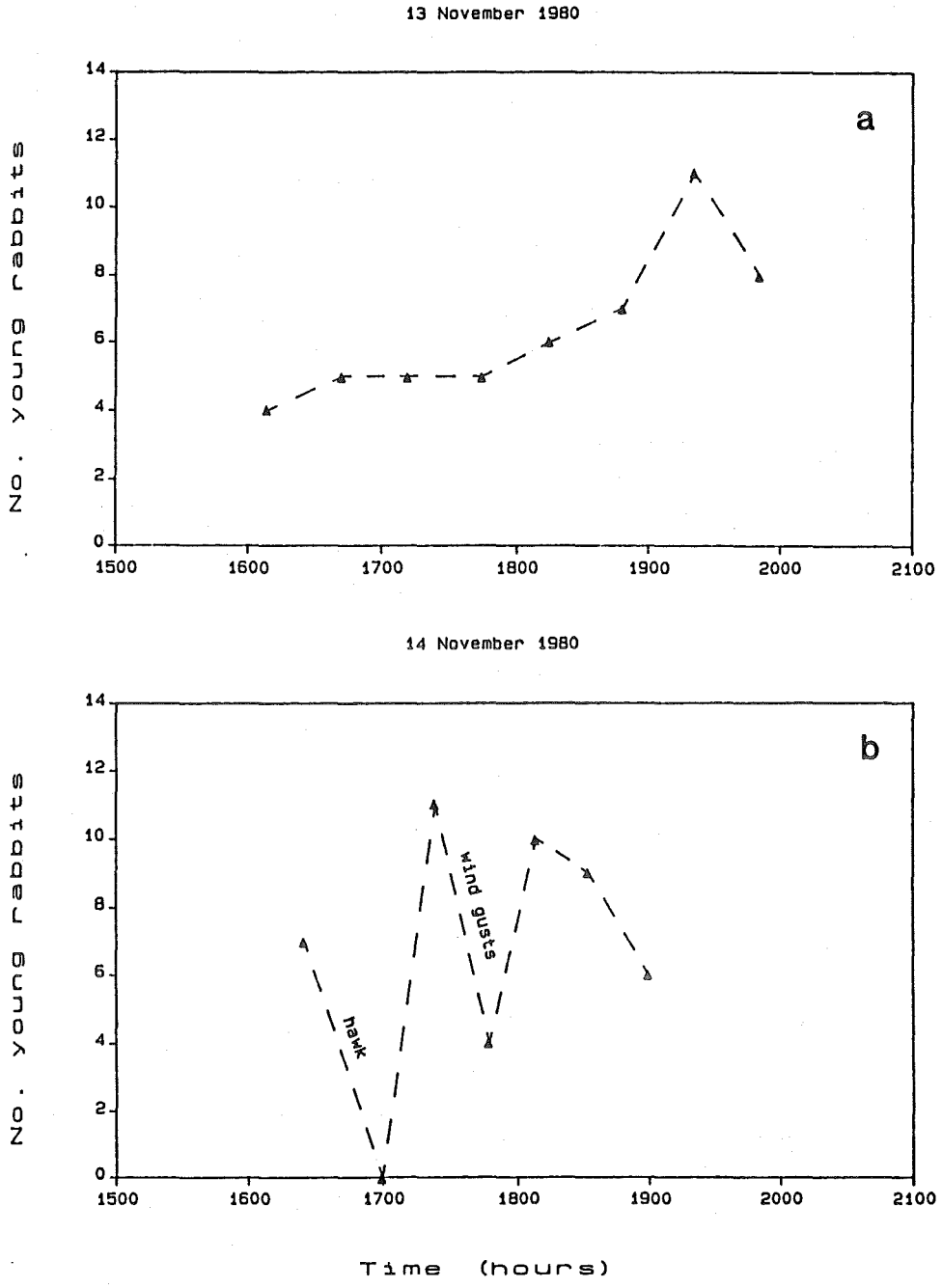
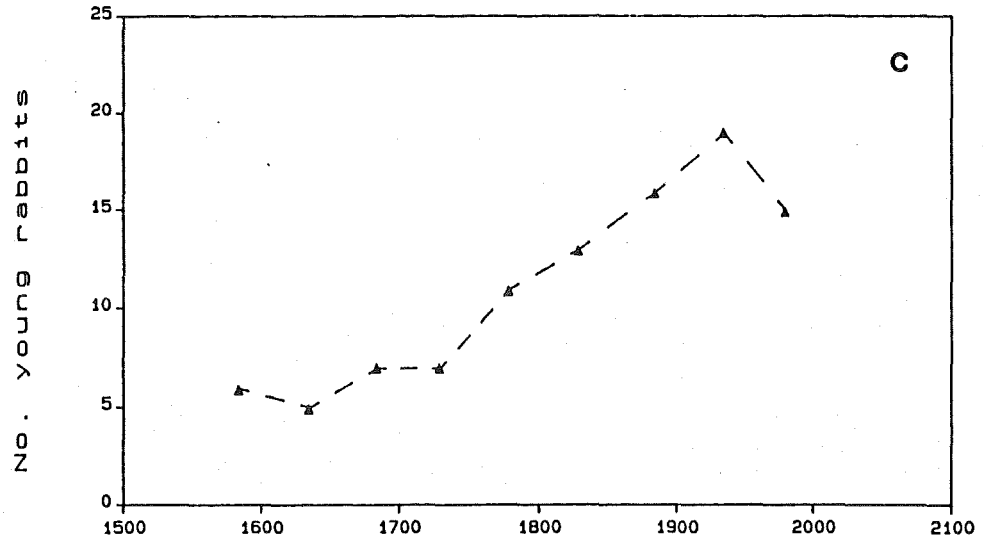
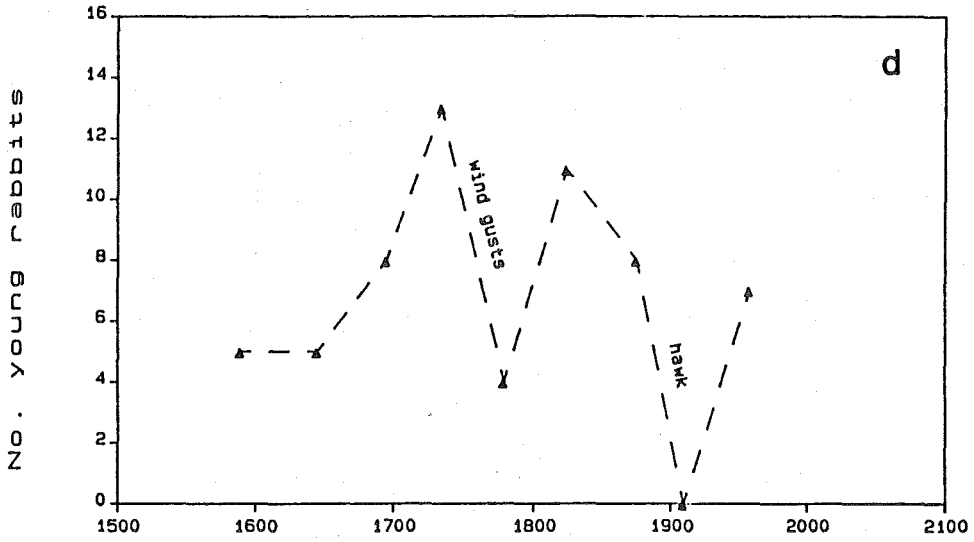


Figure 5.2 (a-e) Effects of disturbance caused by hawks and wind gusts on the emergence of young rabbits on five consecutive days in November 1980.

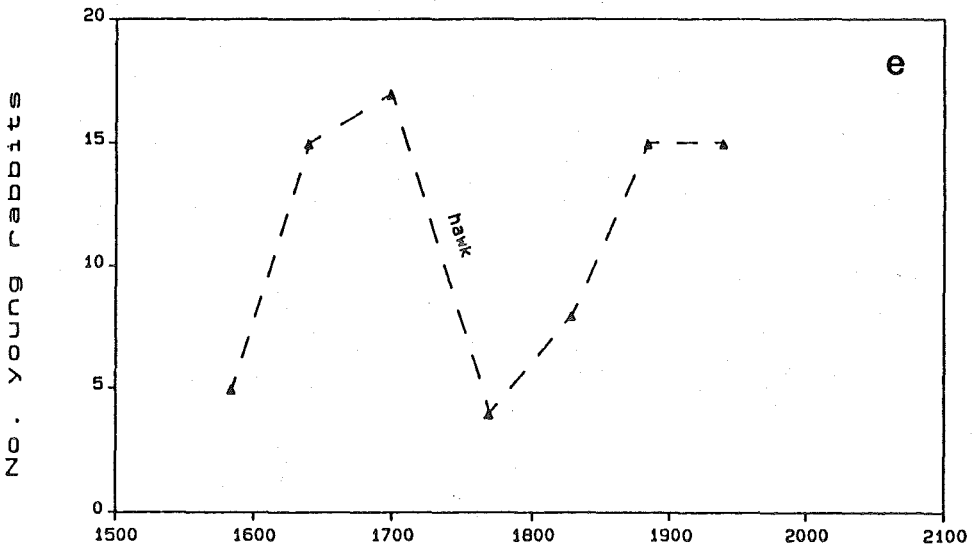
15 November 1980



16 November 1980



17 November 1980



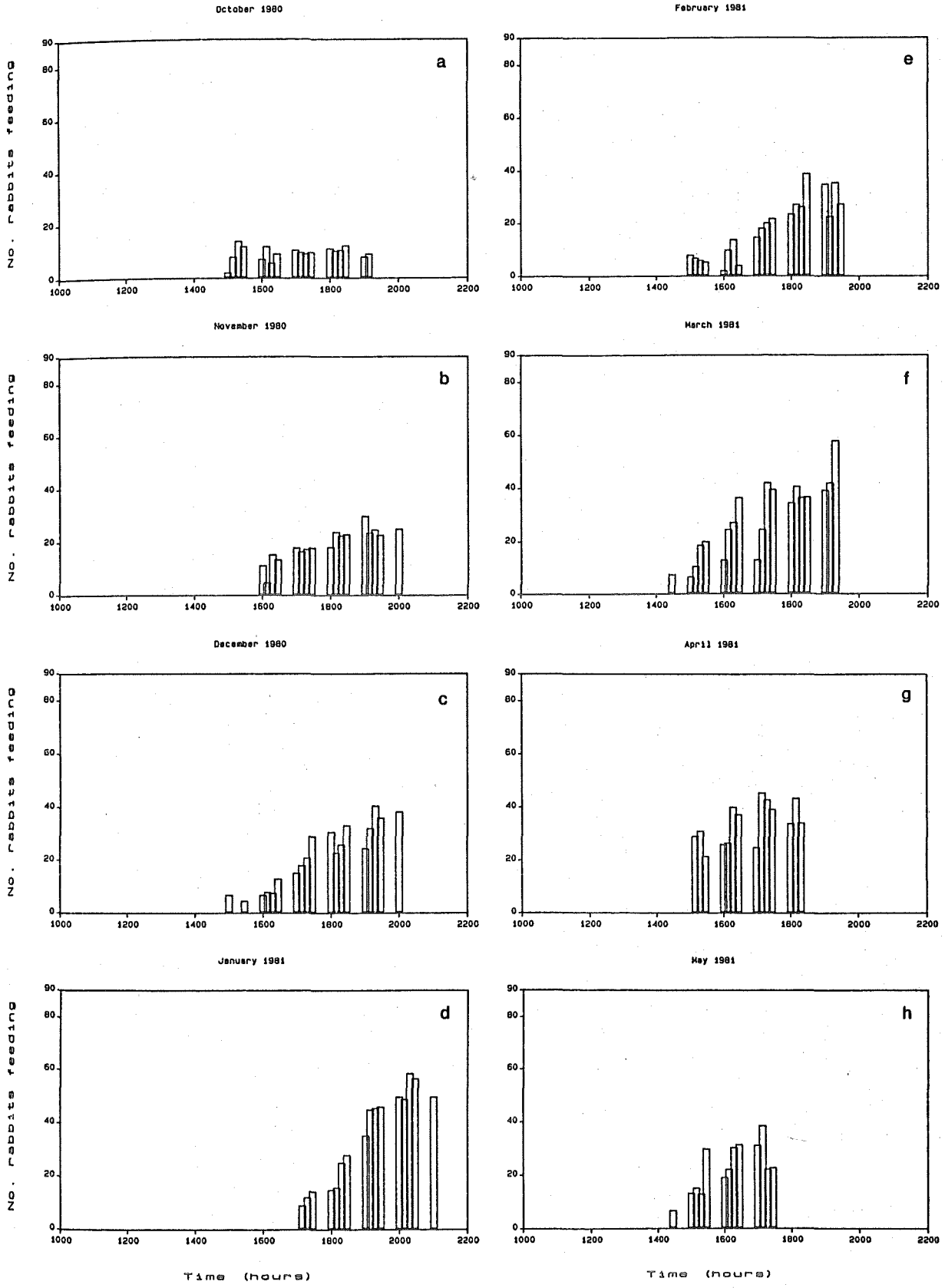
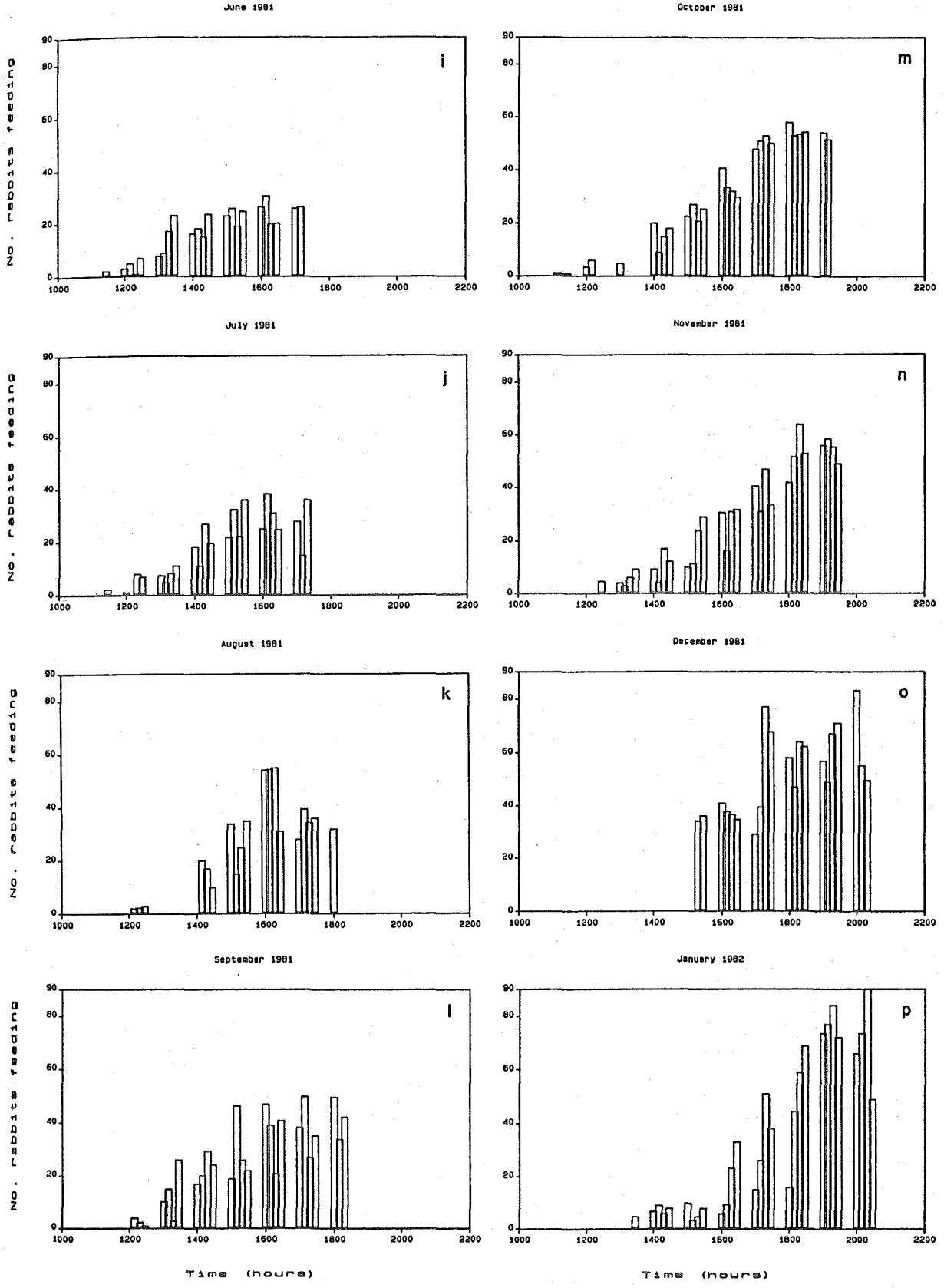
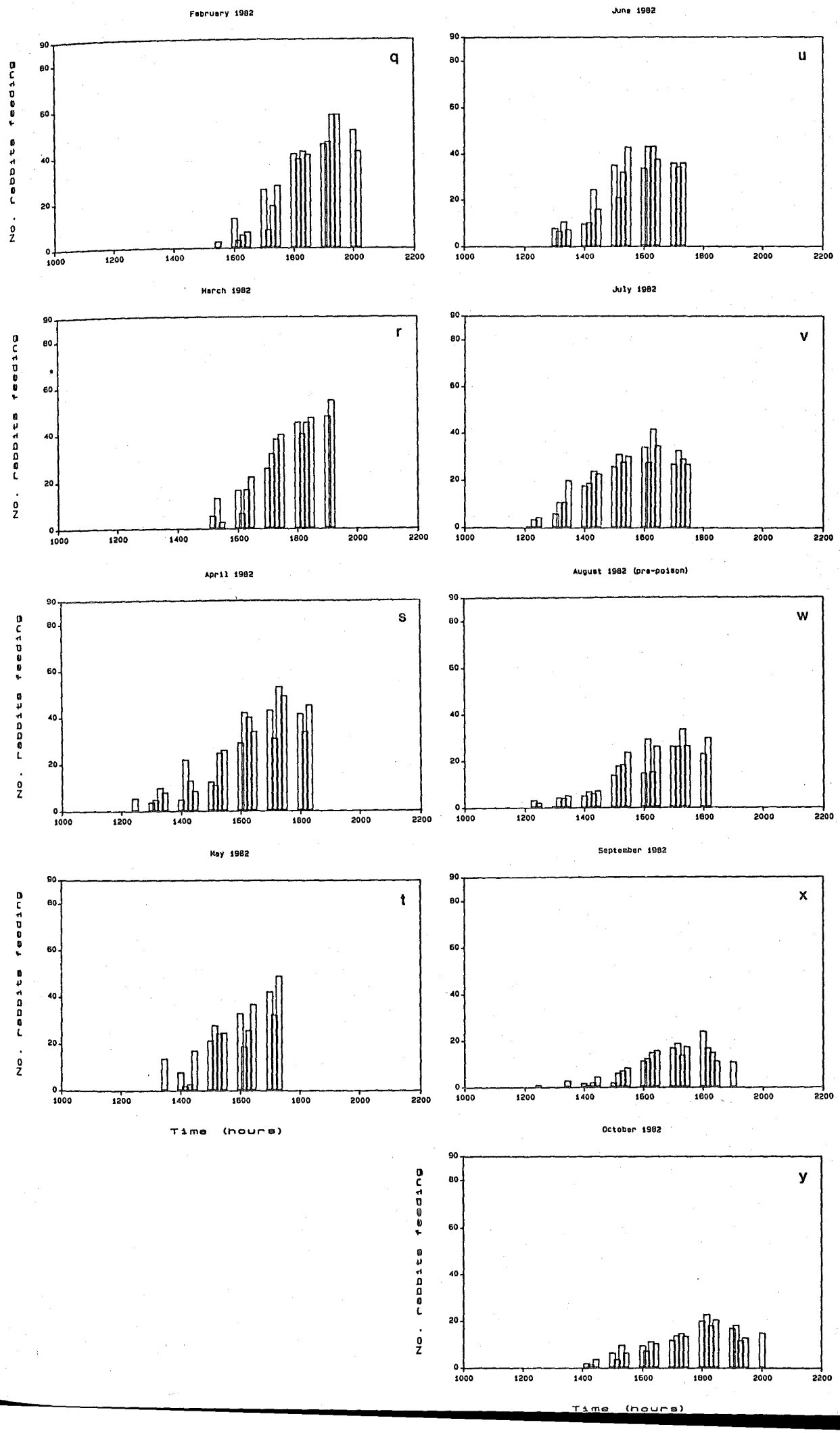


Figure 5.3 (a-y) Monthly emergence patterns as indicated by the number of rabbits feeding, for the period October 1980-October 1982.


June 1981
October 1981
July 1981
November 1981
August 1981
December 1981
September 1981
January 1982
No. rabbits feeding
Time (hours)
i
m
j
n
k
o
l
p


February 1982
q
June 1982
u
March 1982
r
July 1982
v
April 1982
s
August 1982 (pre-poison)
w
May 1982
t
September 1982
x
October 1982
y
No. rabbits feeding
Time (hours)

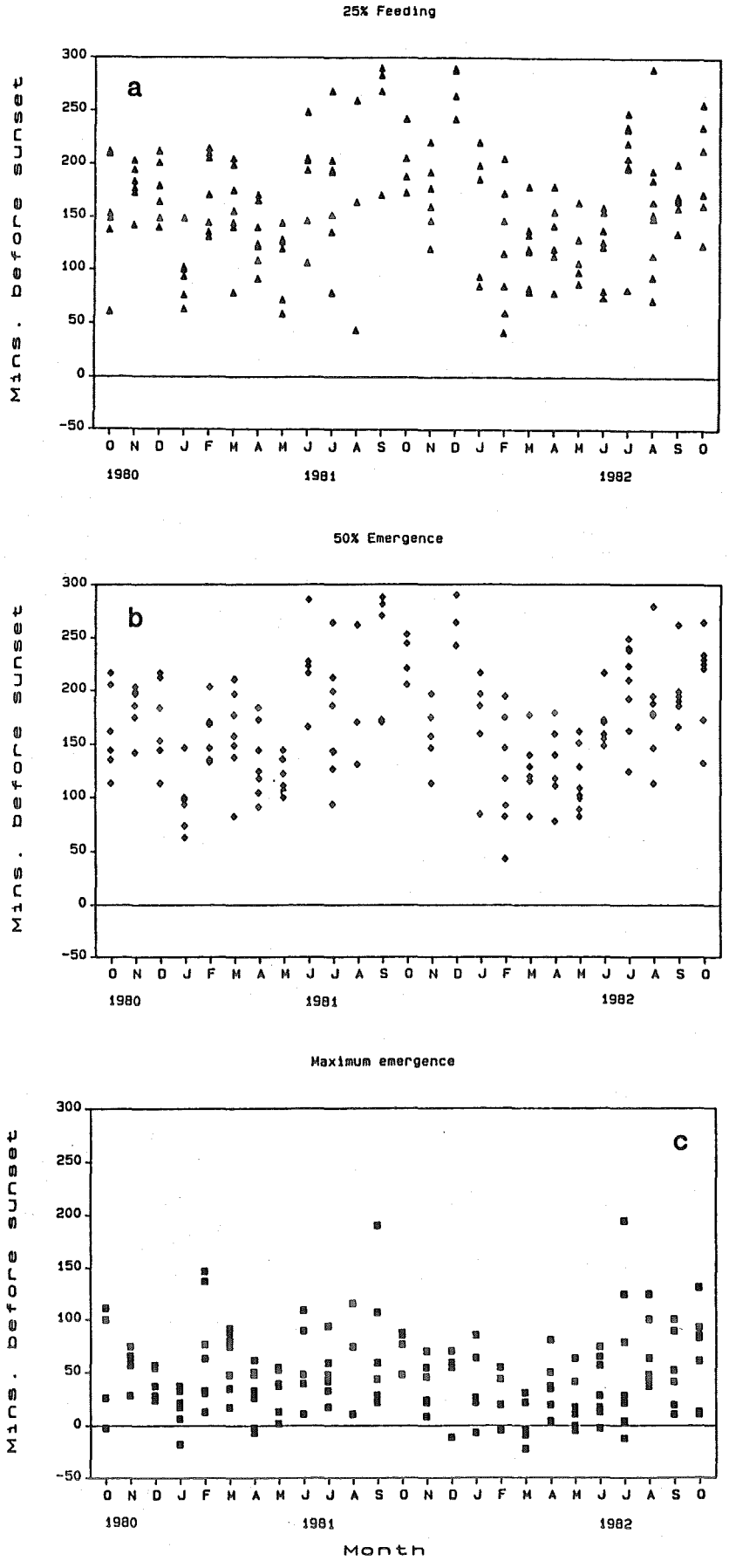


Figure 5.4 Daily emergence times in relation to sunset time for (a) the 25% feeding, (b) the 50% emergence, and (c) the maximum emergence indicators.

The between months variation conformed to a similar pattern for each indicator.

The range over which each level of emergence varied was calculated for each month and pooled by season (Figure 5.5). There was a significant difference in the variability of the three emergence indicators (ANOVA, $F=4.28, p<.05$); emergence based on 25% of the population feeding exhibited the greatest degree of variation while maximum emergence showed the least. The mean range of the daily variation in emergence times was between 70 and 120 minutes in most seasons. Variability of emergence times was noticeably higher in winter than at other times of the year for all three emergence indicators.

When the monthly means of the three indicators are compared with sunset time the overall controlling influence of day length on emergence is evident (Figure 5.6). Even with the considerable within month variability of emergence times, the correlation coefficients for all three indicators with sunset time are very high:

Emergence indicator	n	Correlation coefficient	Significance level
25% feeding	164	0.72	<.001
50% emergence	159	0.77	<.001
maximum emergence	161	0.87	<.001

Nevertheless, other factors must be partly responsible for the large amount of daily variation. The data for the three emergence indicators were correlated with a number of possible influencing variables. Start time and temperature were normally distributed so Pearson correlation coefficients could be used. All the other variables had non-normal distributions and required non-parametric techniques. Kendall correlation coefficients were used as the data contained a large number of tied ranks (Sokal and Rohlf 1969). All variables examined except precipitation were significantly correlated with at least one of the emergence indicators (Table 5.1).

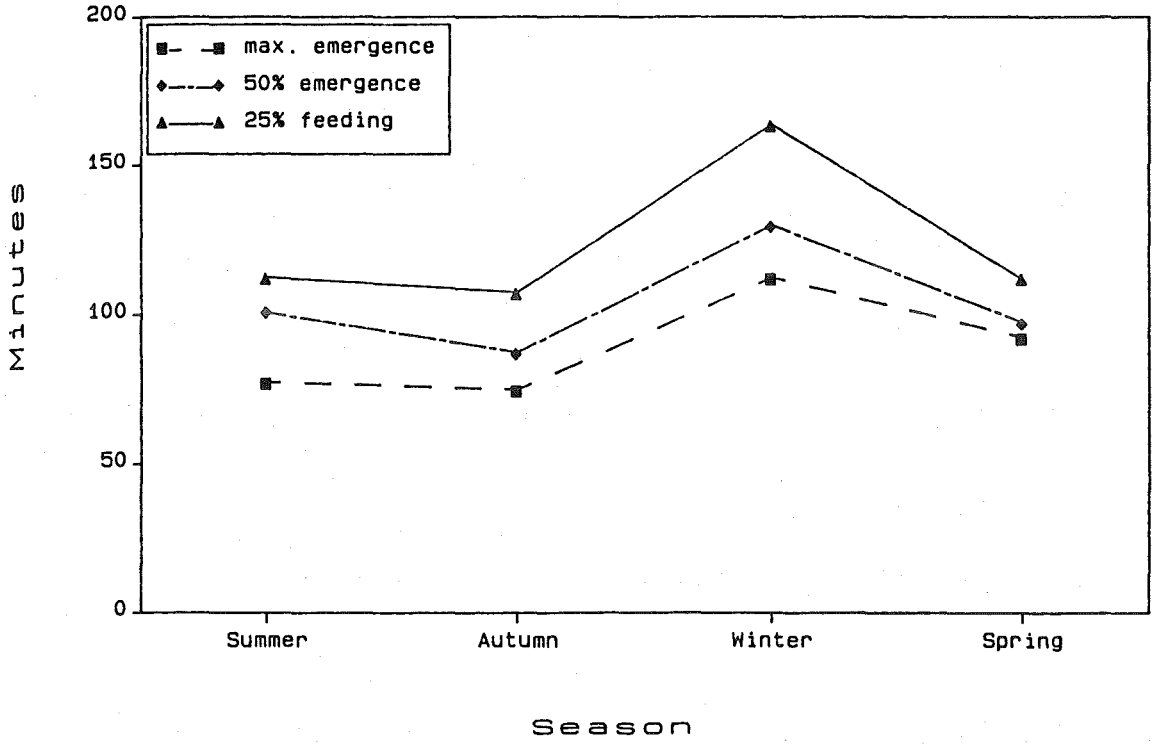


Figure 5.5 Seasonal range in variation of emergence times for the three emergence indicators.

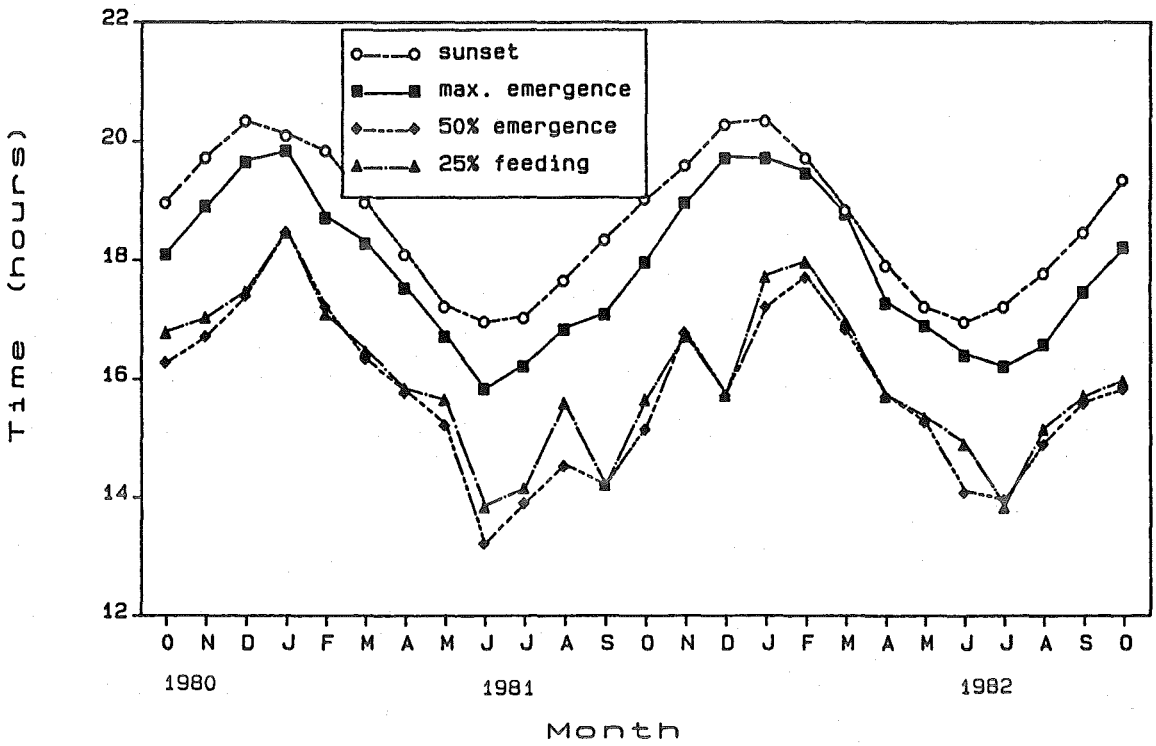


Figure 5.6 Monthly means of the three emergence indicators and their relationship with sunset time.

Table 5.1 Correlation coefficients between the emergence indicators and start time and selected weather variables.

Variable	Level of emergence 25% feeding	50%	100%
Start time	0.56 ***	0.53 ***	0.22 **
Temperature	-0.05	-0.18 *	-0.06
Wind direction	0.12 *	0.16 **	0.01
Wind speed	0.10 *	0.04	0.03
Cloud cover	0.12 *	0.08	0.04
Precipitation	-0.03	-0.07	0.08
n	160	158	164

* p<.05, ** p<.01, *** p<.001

There was a distinct relationship between observation start time each day and all three emergence indicators. As expected, the correlation was highest for the two earliest emergence levels, 25% feeding and 50% emergence. However, even maximum emergence was significantly correlated with observation start time, which usually preceded it by 5-6 hours.

Weather factors also produced significant correlations with the 25% feeding and 50% emergence levels, although at lower significance values. Temperature did not affect the 25% feeding level significantly, but it was significantly correlated with the 50% emergence level as was wind direction. The 25% feeding level was positively correlated with wind speed, wind direction, and cloud cover. As precipitation was recorded on only six occasions no relationship was expected between emergence levels and this factor.

Observations on marked individuals suggest there was a tendency for male rabbits to become active slightly earlier than females, as shown by the monthly means of the 50% emergence level for each sex (Figure 5.7). Although the difference in terms of minutes was usually small, a chi-square contingency test was applied. Comparison of mean values for each sex was impossible

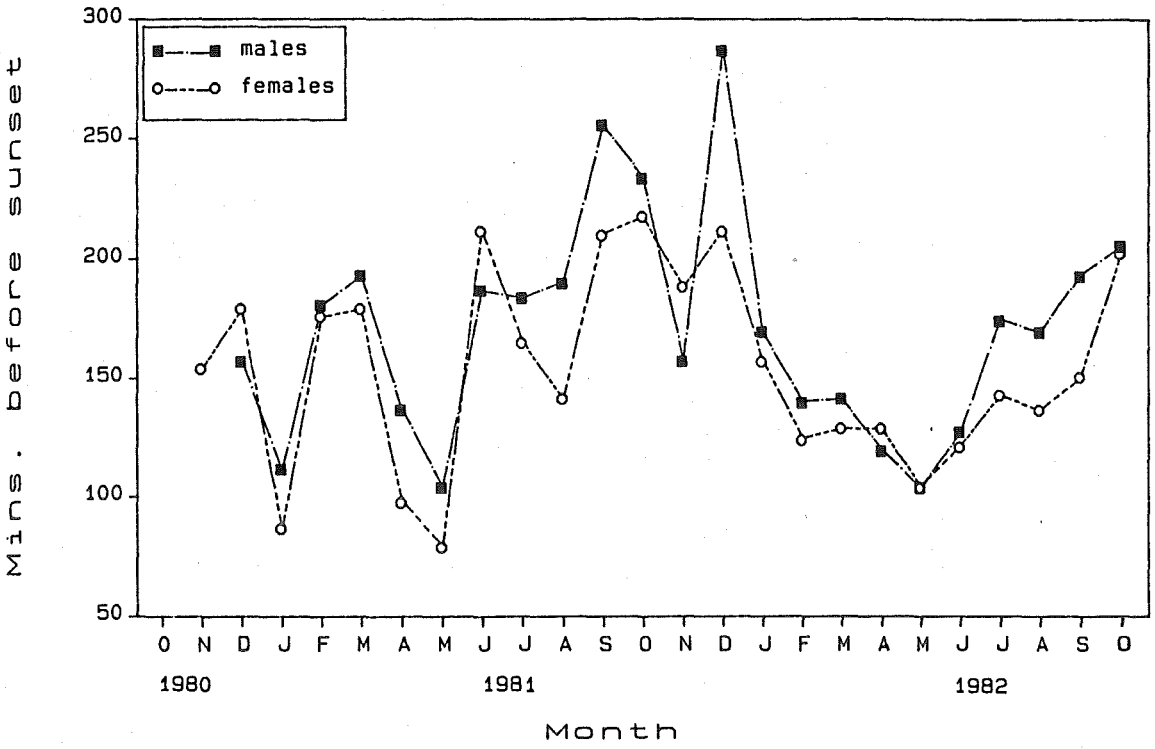


Figure 5.7 Mean monthly time of 50% emergence for male and female rabbits.

because sex differences were obscured by the large amount of daily variation, due to factors previously mentioned. Therefore, the transect sampling data were examined with respect to which sex, if any, reached the 50% emergence level first. If no difference in emergence time existed between the sexes the expected ratio should be 1:1:2 for males first, females first, and both sexes equal respectively. The observed and expected ratios were:

	First to reach 50% emergence level		
	Males	Females	Both sexes
Observed	62	37	65
Expected	41	41	82

The difference between the observed and expected ratios was highly significant (chi-square=14.67, $p<.001$) and supports the view that generally males became active slightly earlier than females.

5.3 Discussion

The pattern of emergence found in this study, a steady rise in numbers throughout the afternoon, differs somewhat from previous findings on emergence. Both Dunnet (1957b) and Fullagar (1981) found that in the rabbit populations they studied in Australia, emergence was usually characterised by a sudden increase in the numbers of rabbits above ground and active. However, Gibb et al. (1978) reported a more gradual build-up of rabbit numbers during the afternoon emergence period in the Kourarau enclosure study in the Wairarapa, North Island. One notable feature of the present study is that most adult rabbits on the Butchers Dam study area had their permanent resting locations outside the observed area. Consequently, the activity data do not strictly represent emergence effects but rather the time at which rabbits became more active and moved down from their resting places to feed. However, further observations revealed that once they appeared on the surface, most

rabbits did not linger long before moving down onto the observed area.

Unlike adult rabbits, many of the young present were resident within the observed area where most of the breeding burrows (stops), as well as numerous abandoned burrows, were located. Young rabbits generally emerged later than adults and reached their maximum emergence level slightly earlier. This apparent difference was partly due to some adult rabbits not moving onto the observed area until just before dusk. Also, it is doubtful whether the majority of young rabbits were ever active at the same time. In their first few weeks above ground young rabbits were mostly involved in exploratory activities and time spent feeding was minimal. With frequent disturbances young rabbits often sought cover below ground in the breeding stops or unoccupied burrows. This caused erratic fluctuations in the numbers of young in view on many occasions, a feature also encountered by Dunnet (1957b), Gibb et al. (1978), and Fullagar (1981). Adult rabbits, however, sought cover only from major disturbances such as human presence, so successive transect counts for adults were more uniform.

The most noticeable seasonal feature was the earlier emergence of rabbits during winter and spring in relation to sunset time. Rabbits began feeding earliest in spring with the 25% feeding level being reached about three hours before sunset. In contrast, this level was reached approximately one hour later in the autumn months. A number of factors, including the incidence of breeding in the population and the availability of food resources, would be interacting to produce these differences. Earlier emergence in winter months may also indicate a trend towards a bimodal distribution of activity with peaks around sunset and sunrise. In this way rabbits could avoid being active during the coldest hours of the night when energetic benefits from a reduced food supply would be marginal. At other times of the year when conditions were milder, activity would tend towards the single nocturnal peak of activity reported by other workers (Mykytowycz and Rowley 1958, Gibb et al. 1978).

Energetic factors may have also been responsible for the overall trend towards earlier emergence in the second year of the study. More rabbits were present during the second year and a larger population would create an increased demand upon the food supply. Rabbits needed to forage for longer to maintain the required level of food intake (Gibb et al. 1978).

The three emergence indicators examined illustrate the highly variable nature of the rabbit's onset of activity reported elsewhere (Dunnet 1957b, Rowley 1957b, Fullagar 1981). Variation was greatest for the 25% feeding and 50% emergence levels where proximate factors were responsible for considerable daily fluctuation. The overall controlling influence of the ultimate factor, day length, is clear from the high correlation coefficients between sunset time and all three emergence indicators. Although observation start time is significantly correlated with the emergence indicators, the relationship is somewhat artificial as the start times were usually chosen subjectively to coincide with the onset of activity in the population each day. However, small differences in start times did account for some of the daily fluctuations in emergence levels through disturbance effects on the population.

Relationships between the emergence indicators and the proximate weather variables are far from simple, particularly because of the high correlations between several of the weather variables themselves. Emergence times are a product of the influence of all these variables and other exogenous factors, as well as endogenous factors within the population itself. Pooling information from many days and different seasons is likely to obscure possible relationships and bias conclusions. However, a number of generalisations are possible. Bad weather, characterised by lower than normal temperatures and strong southerly winds, usually delayed the onset of activity regardless of season. Although a specific chill factor was not calculated from temperature and wind data, the relationship between emergence times and such a synergistic factor is likely to be strong. Very high temperatures associated with little or no wind had a similar effect during the summer months. Under these very hot

conditions rabbits would appear but remain inactive, resting in the shade of rocks or vegetation, until temperatures began to decrease around sunset when they would begin to feed.

Although it was not statistically correlated with precipitation, emergence was generally later when precipitation occurred, especially if it was heavy or associated with low temperatures and southerly winds.

Checks with the number of marked rabbits known to be present revealed that almost invariably the whole population had emerged before sunset. Similarly, Gibb et al. (1978) found that 85% of the population they studied in the North Island had usually emerged by dusk. Lower levels of emergence during daylight hours have been reported in Great Britain and Australia (Southern 1948, Dunnet 1957b, Rowley 1957b). Besides differences in habitat suitability, with more marginal conditions in Central Otago imposing a higher food stress on rabbits, the higher numbers of predators in Great Britain and Australia (Soriguer and Rogers 1981) could help to explain the lower levels of diurnal activity in these countries.

The trend for male rabbits to become active slightly earlier than females has not been documented elsewhere. The difference in emergence times between the sexes was most noticeable during the period June to October. This included the period prior to and the early stages of the breeding season, when territoriality and social effects are greatest. At this time of year male rabbits are more highly motivated towards preserving the integrity of their spheres of influence, based not only on females but also on preferred feeding areas (see section 7.2.2). Apparently this increased level of activity on their part led to slightly earlier emergence times.

6 ACTIVITY BUDGETS

6.1 Introduction

Numerous studies on the rabbit have shown that the surface activity period usually begins in the late afternoon and continues throughout the night, ending one or two hours after sunrise (Southern 1940, Mykytowycz and Rowley 1958, Gibb et al. 1978, Fullagar 1981). This pattern is common among the lagomorphs as studies of cottontail rabbits (Lord 1961, 1964), snowshoe hares **Lepus americanus** (Mech et al. 1966), mountain hares **L. timidus** (Bayfield and Hewson 1975), and European hares **L. europaeus** (Flux 1981b) have shown.

Logistical limitations in this study restricted most observations to daylight hours. The necessity of collecting as much information as possible on a variety of social behaviours helped determine that late afternoon observations would be the most productive. The frequency of occurrence of some of the more significant behaviours, such as reproductive and aggressive behaviours, is highest around this time (Fullagar 1981). The overall level of activity around dusk is also less variable than at other times of the day (Dunnet 1957b, Gibb et al. 1978) and was therefore more likely to give consistent results.

Although the possibility of night-time observations using a spotlight was considered, previous evidence (Gibb et al. 1978) suggested that results obtained would not be reliable as rabbits often changed from one activity to another when a spotlight was shone on them. In contrast, the Zeniscope (night vision system) which did not cause any disturbance to the rabbits was useful in providing a limited number of early evening observations.

Results and discussion for each of the behaviour categories are presented in the next section. In addition, a general discussion follows which emphasizes the most important features of the activity budget results, including the variation between different segments of the population.

Together with the following two chapters, this chapter provides a profile of the rabbit's behaviour during the peak period of activity, its social organisation, and movement patterns in habitat typical of much of Central Otago.

6.2 Results and Discussion

An overall indication of the frequency of occurrence of activity in the 10 behaviour categories can be obtained by examining the data collected during transect sampling (Table 6.1). For convenience the monthly data samples have been pooled by season. Marked trends are evident in the number of observations recorded for each category. Feeding and resting behaviour accounted for approximately 75-85% of all observations, whereas reproductive, territorial, aggressive, and displacement behaviour together only made up about 3% of transect sampling observations.

Table 6.1 Frequency of occurrence of observations in the 10 behaviour categories for transect sampling.

		Percent of observations									
Season	n	Miscellaneous	Feeding	Grooming	Resting	Locomotory	Alert	Reproductive	Territorial	Aggressive	Displacement
Spr 80	2533	0.8	60.6	3.9	15.6	11.1	2.2	3.0	0.7	2.1	0.1
Sum 80/81	5485	0.3	65.5	4.5	17.6	9.0	1.4	0.4	0.4	0.8	0.1
Aut 81	5417	0.3	67.6	4.9	13.8	8.4	1.5	0.4	0.4	2.6	0.2
Win 81	4518	0.1	61.8	6.2	19.7	6.9	1.6	0.8	0.6	2.1	0.2
Spr 81	6238	0.1	67.0	4.8	18.4	4.9	1.1	1.4	0.5	1.8	0.2
Sum 81/82	6554	0.1	65.9	5.0	21.2	5.0	1.2	0.2	0.3	1.0	0.1
Aut 82	4734	0.0	67.9	4.7	20.6	5.0	0.5	0.3	0.1	0.9	0.0
Win 82	7642	0.1	61.6	4.0	24.6	6.0	0.7	0.7	0.6	1.2	0.3
Spr 82	3221	0.1	59.5	4.9	26.1	5.7	0.8	1.0	0.7	1.0	0.3
Total	46342	0.2	64.5	4.8	19.9	6.6	1.2	0.8	0.4	1.5	0.2

n = number of observations

Although there appears to be little variation between the seasons in the percent of observations recorded in each behaviour category, significant differences do exist but these have been masked by pooling the data. Variation arises from factors such as sex, age, and social status differences between individuals, and time of day. These differences will become apparent when each of the behaviour categories is dealt with in the following sections.

In the first and second months of the study, observer inexperience led to some unusually high values for the number of observations in several behaviour categories, notably the miscellaneous, alert, and reproductive categories. Where these values are significantly different from those recorded during the remainder of the study, they have been omitted from graphs and numerical analyses. Also, it is important to remember that many of the studies with which these results are compared were based on either continuous 24-hour surveillances or dawn to dusk watches (e.g. Mykytowycz and Fullagar 1973, Gibb et al. 1978, Fullagar 1981). Consequently, any lack of close agreement with other studies may not necessarily indicate a behavioural difference, but rather reflect the effects of different sampling periods. Relative differences within the population in relation to features such as season, sex, and social status are more important than minor variations in comparison with previous studies.

6.2.1 Behaviours in the miscellaneous category

The miscellaneous category included four behaviours associated with burrows (viz. entering, emerging from, looking down, and digging) as well as defecating and urinating. All of these behaviours were infrequent and, except for digging, of very short duration. From a total of 46,342 behaviour observations during transect sampling, only 85 (0.18%) belonged to the miscellaneous category. This result is confirmed by the information from focal sampling, where miscellaneous behaviour comprised 0.14% of the total focal sample time.

Although entering, emerging from, and looking down a burrow are all easily recognisable activities, they are usually of short duration (less than 5 seconds) and transitory (i.e. they occur in the context of some other behaviour, most commonly locomotory). Observations of these activities were spread fairly evenly amongst young and adult rabbits, and between the two sexes. In contrast, digging behaviour was a complete activity in itself and frequently of considerable duration (e.g. on one occasion an adult female rabbit, F02, was observed digging almost continuously for 10 minutes).

Transect sampling revealed occurrences of digging in all seasons, although the total number of occasions when digging was recorded (n=16) is too low to show any definite seasonal variation. However, when the seasonal totals for each of the behaviours associated with burrows are pooled, a bias towards spring months (40% of observations) is revealed. In focal samples digging activity was observed in winter and spring months only, a period which corresponded to the initial stages of the breeding season for the population. Although Gibb et al. (1978) recorded digging during all seasons of the year, they found a peak during winter and spring months also.

Not unexpectedly, females spent longer engaged in digging (0.23% of focal sample time) than males (0.05%), a feature noted by Lockley (1961). Examining the focal sample data for winter and spring months revealed that, amongst females, social status was related to the amount of time spent in this activity. Dominant females spent 0.80% of their time digging during this period, compared with 1.73% for subordinate females. Most digging was probably associated with the construction of breeding burrows or 'stops'. Dominant females generally use established burrows while subordinate females more commonly dig isolated breeding stops (Mykytowycz 1959, 1960). Mykytowycz and Gambale (1965) showed that the frequency of appearance of breeding stops increased with the progress of the breeding season as more subordinate females commenced breeding.

Rabbits at Butchers Dam spent less time digging than those at Kourarau, Wairarapa (Gibb et al. 1978). A survey of the burrows and digging sites on the observed area at Butchers Dam in April 1983 revealed that the number of burrows in use (8.0 per ha) was markedly less than at Kourarau (134.1 per ha). Whereas the coarse skeletal soils over much of the Kourarau area were well suited to burrowing (Gibb et al. 1978), digging was difficult or impossible over much of the Butchers Dam area as the distribution of digging sites shows (Figure 6.1).

Burrows were classified as either 'used' or 'unused'. The latter were easy to identify as frequently they were overgrown or had cobwebs just inside the entrance. Burrows less than 1 m long were classified as 'short burrows'. Sometimes a burrow would consist of a tunnel 1-2 m long with an entrance at each end; these were termed 'run-throughs'. Finally, where digging had occurred but only to a depth between 10 and 30 cm, the sites were classified as 'starts'. The frequencies with which each of these features occurred are presented in Table 6.2.

Table 6.2 Frequency of occurrence of the different types of digging sites on the observed area (approx. 4 ha) at Butchers Dam.

Type of digging site	No. counted	% occurrence
Burrow - used	28	7.8
Burrow - unused	33	9.1
Short burrow (<1 m)	160	44.3
Start (10-30 cm)	85	23.6
Run-through	55	15.2

A large number of digging sites (67.9%) were abandoned while the burrow was still less than 1 m long, probably due to the rocky nature of the substrate. Run-throughs were usually formed where burrowing rabbits had encountered rock and changed their direction of digging only to reappear at

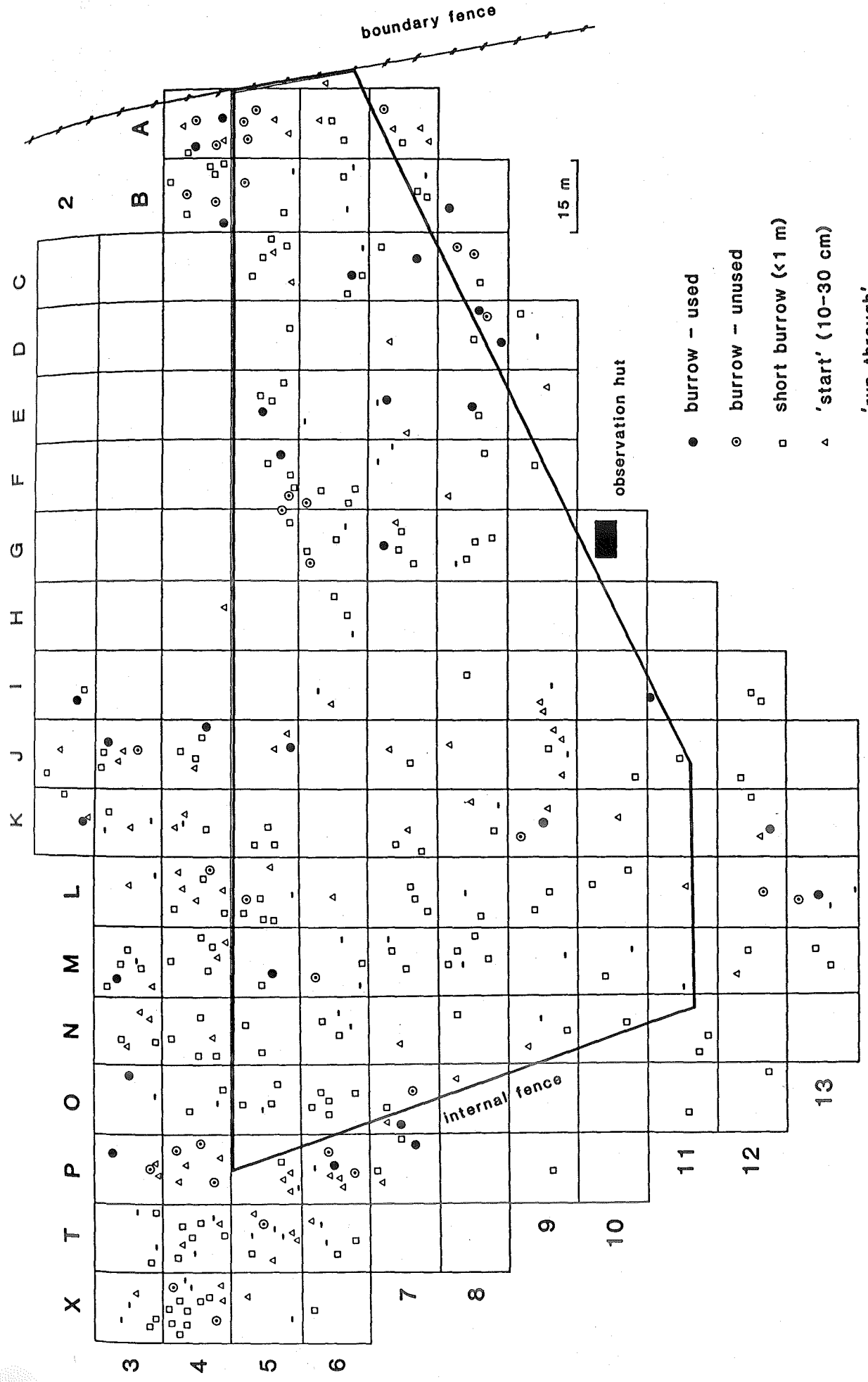


Figure 6.1 Distribution of digging sites on the Butchers Dam study area.

the surface. The number of run-throughs counted on the study area was extremely high compared with other areas in New Zealand (pers. obs.). They were used frequently both by young and adult rabbits, and were especially useful as shelters to take refuge in when hawks were present. Although the survey of burrows and digging sites was conducted only once, no major differences in the proportion of sites in each category would be expected at other times of the year. A small increase in the number of used burrows may occur during the breeding season and immediately following it, as initially some females use abandoned burrows as breeding stops and latterly when young rabbits begin to disperse.

When digging occurred, it was generally for an appreciable length of time. However, rabbits engaged in digging frequently paused and assumed an alert posture; most commonly this would be a crouch or upright stance from which they would survey the surrounding area. A rabbit with its head down and digging is more susceptible to predation which explains the high level of alertness. Alert behaviour could also be associated with the individual's level of territorial confidence. As digging rabbits were often subordinate females, their frequent stops to scan the area may have reflected lack of confidence at a particular site as well as guarding against predation.

Defecating was never observed, while urinating was seen only twice, both times during transect sampling. Coprophagy and enurination are not included in the miscellaneous category; they are more appropriately classified within the feeding and reproductive categories respectively. In a field situation defecating and urinating are difficult to observe except from very close range. There were numerous instances when rabbits adopted a posture that suggested either of these activities but, because urine or faeces could not be seen, they were not recorded.

6.2.2 Feeding behaviour

Four behaviours were identified within this category (viz. grazing, browsing, scratch feeding, and coprophagy). Southern's (1940) division of grazing into three levels (i.e. casual, normal, and voracious feeding) was not followed here because it was considered too subjective. The feeding category constituted, by far, the majority of behaviour observations comprising 64.5% of transect sampling observations and 61.2% of focal sample time. In most months the number of observations in the feeding category was 60-70% for transect sampling (range: 57-75%), whereas focal sampling results were more variable (range: 46-82%). Frequent pauses were noted during feeding behaviour, when the rabbit would look around or move a short distance (generally less than 1 m), a feature also observed by Southern (1940). However, no change in behaviour was recorded as the rabbit usually continued chewing, implying that such behaviour was a normal part of feeding activity. Grazing formed the bulk (>95%) of all feeding observations for both sampling methods. Scratch feeding comprised 2-3% of feeding activity compared with 1% for browsing. Coprophagy was even rarer, comprising only 0.1% of all feeding observations for both transect and focal sampling.

The pattern of feeding noted in many previous studies (e.g. Southern 1940, Mykytowycz and Rowley 1958, Gibb et al. 1978), where rabbits feed initially around their warrens or resting places and subsequently move further afield, was not seen here. The main factor responsible for this difference was the heterogeneity of the habitat. Very few rabbits had resting locations within the preferred feeding areas. Instead, most rabbits had resting locations in the sparsely vegetated, rocky outcrops on the eastern edge of the study area, necessitating considerable daily movements onto the central part of the area where vegetation was more abundant.

Among the most important factors determining the amount of feeding behaviour are the quantity and quality of food available. Results from stereoscopic analysis of vegetation plot photographs indicate that these

factors were not constant (Figure 6.2). Unfortunately, vegetation data are only available for the period June 1981-October 1982. Within this interval live vegetation levels were greatest in winter and spring of 1981 and spring of 1982. At these times live vegetation comprised approximately 30-40% of total ground cover. In the intervening period the percent cover of live vegetation was considerably less, reaching a minimum of 11% in summer 1981/82. As expected, the levels of dead vegetation cover and bare earth changed in accordance with fluctuations in the amount of live vegetation.

There was a strong correlation between the levels of the various ground cover categories and the amount of browsing and scratch feeding (see Figure 6.2). Commonly browsed plants included thyme, briar, speargrass, and thistles, while scratch feeding was a means of obtaining plant roots. These two feeding activities were more frequent when the food supply was lowest. However, this relationship was significant only when data for spring 1982 had been excluded from the analysis. Although the level of live vegetation cover for spring 1982 was high, which would normally indicate a relatively low level of browsing and scratch feeding, much of this was due to a flush of stonecrop, a relatively unpalatable species (pers. obs.) which would not contribute any significant amount to the food supply.

In general, feeding on stonecrop and another unpalatable species, scabweed, occurred only during late autumn and early winter months when the preferred plant species were severely depleted. Observations of rabbits feeding on stonecrop suggest that the growing tips were favoured, possibly because these may contain lower concentrations of the chemicals that make the other parts of this plant relatively unpalatable (Clapham et al. 1968). As the live vegetation cover increased the proportion of feeding activity comprised by browsing and scratch feeding decreased ($r=-0.93, p<.05$). Similarly, the relationship between the frequency of these two activities and the proportion of ground cover composed of dead vegetation and bare earth was significant ($r=0.91, p<.05$). Southern (1940) reported that during winter the incidence of

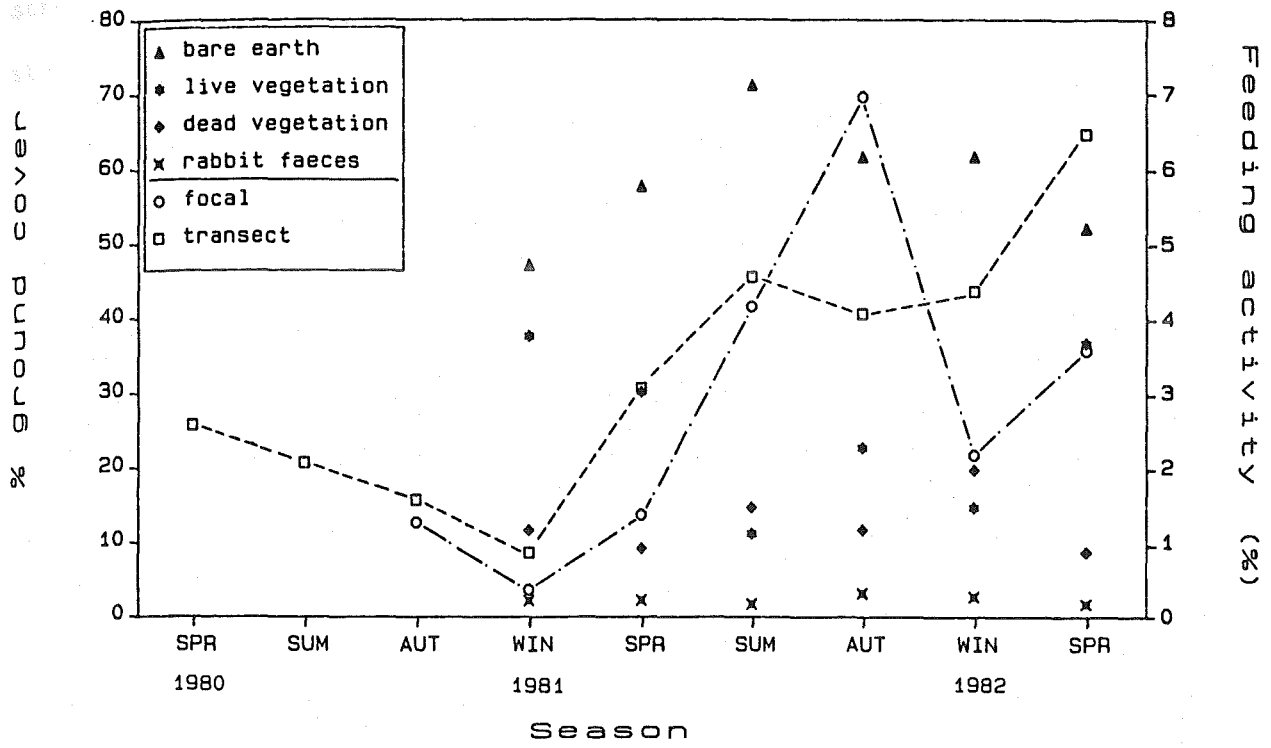


Figure 6.2 Seasonal details of ground cover compared with the level of browsing and scratch feeding activity observed during transect and focal animal sampling.

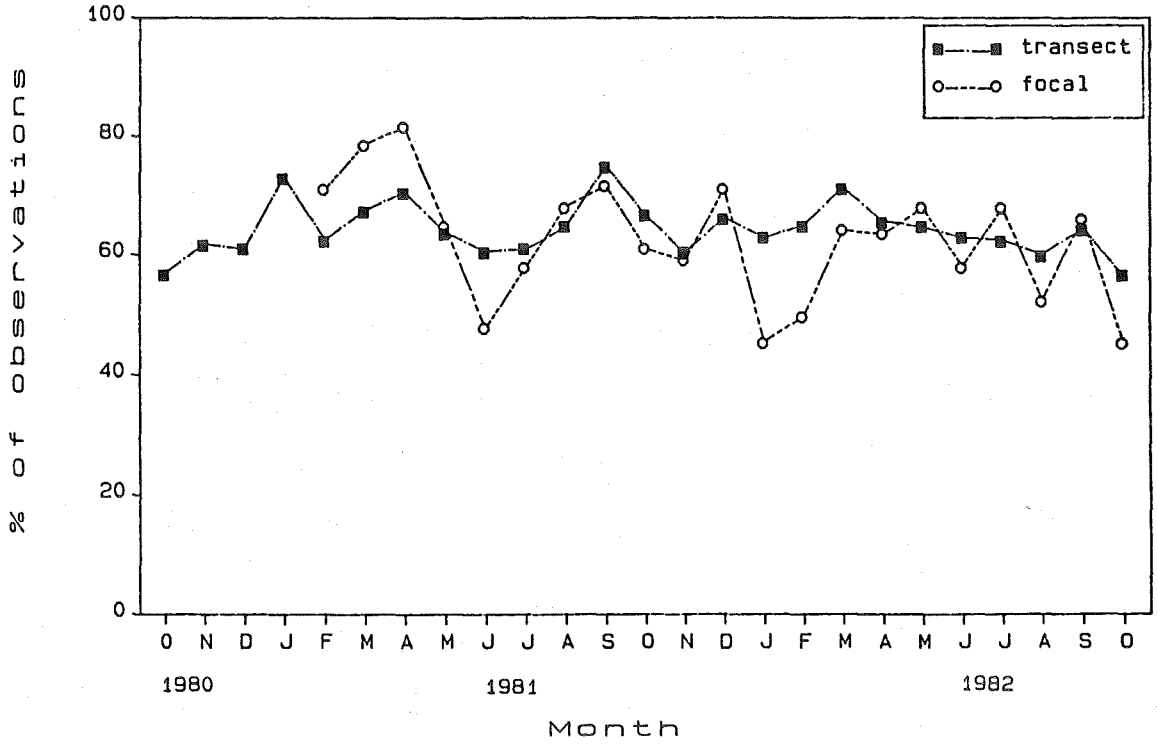


Figure 6.3 Monthly levels of feeding behaviour indicated by transect and focal animal sampling.

scratch feeding and browsing increased markedly in the rabbit population he studied.

Coprophagy was seen only occasionally: 23 times during transect sampling and 32 times during focal sampling. It often continued for several minutes with the rabbit, always in the sitting position, taking a faecal pellet about every 10–15 seconds. Coprophagy was almost totally restricted to adult rabbits; only one young rabbit was observed reingesting faecal pellets. The number of observations of coprophagy for male and female rabbits were similar. No seasonality was evident in the results although the sample may be too small to show any variation.

The monthly variation in the overall level of feeding behaviour does not follow a distinct pattern (Figure 6.3). Nevertheless, increases and decreases between consecutive months are reflected in both types of sampling data, confirming that the apparent lack of any seasonal pattern is not due to the vagaries of one particular sampling method. Lack of seasonality in the feeding results could be due to the effects of a number of factors (some of which may interact with each other), such as the presence of young in the population, changes in the population density, changes in the food supply, or variation in other activities. Some features of the feeding category can be identified when particular groups within the population are examined separately.

The amount of time spent feeding is much less variable for adults than for young rabbits (Figure 6.4). Young rabbits are usually present from October through to April. Transect sampling observations revealed that during this period adult rabbits spent about 60–70% of their time feeding. Young rabbits, on the other hand, while spending considerably less time feeding than adults in the first few months (October–December), spend more time feeding than adults during the following months (January–April). In both years (1980/81 and 1981/82) young rabbits spent significantly more time feeding (Mann-Whitney U-test, $p<.05$) in the latter part compared with the early part of this period.

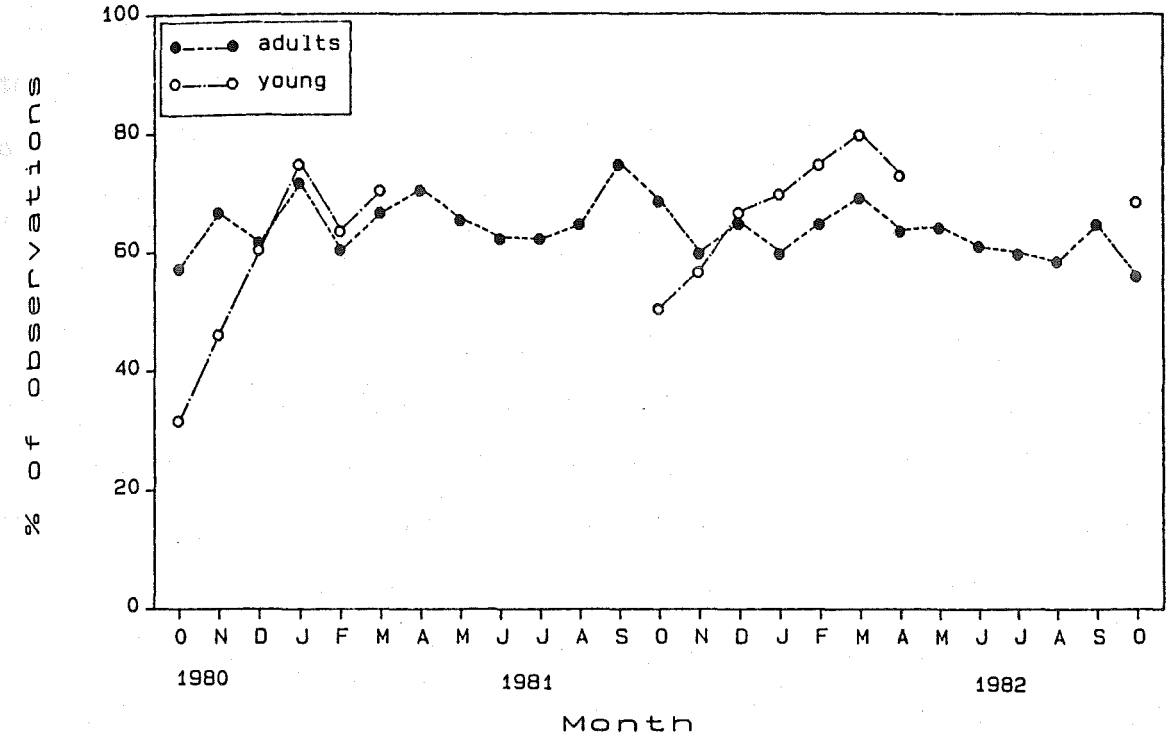


Figure 6.4 Amount of time spent feeding by young and adult rabbits (transect sampling).

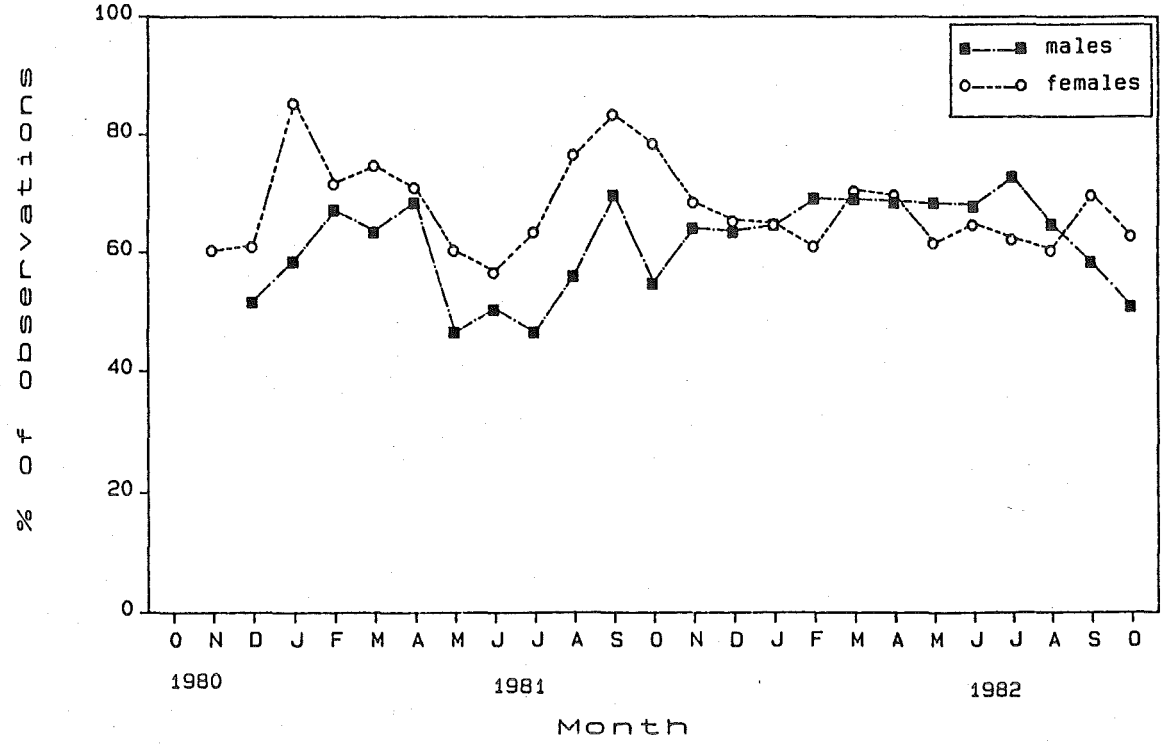


Figure 6.5 Amount of time spent feeding by adult male and female rabbits (transect sampling).

Another difference existed within the feeding data for young rabbits, this time between the two years. The level of feeding activity was higher during the 1981/82 season compared with 1980/81. The population size was greater during 1981/82 (see section 9.2.5) and may have necessitated an increase in time spent feeding in order to satisfy growth and maintenance requirements. A similar trend for adult rabbits was not evident, suggesting that the effects of increased population density and the resulting pressure on the food supply was not as critical for adults as for young rabbits. A similar result has been described by Gibb et al. (1978) for rabbits in the Kourarau enclosure.

Male rabbits spent less time feeding than females (approx. 62% of transect sampling observations, cf. 68% for females), although in autumn and winter of 1982 this trend was reversed (Figure 6.5). Nevertheless, a paired t-test for all months still revealed a significant difference ($t=3.08, p<.01$) between males and females. Focal data exhibited an almost identical pattern. The greatest difference in the amount of feeding behaviour between male and female rabbits was found during spring months (Table 6.3). The difference during spring was approximately three times the difference at other times of the year. The most likely explanation is the increased energy requirements of pregnancy and lactation for females during the breeding season. Mykytowycz and Rowley (1958), in their enclosure study of a population of wild rabbits, noted that pregnant females and juvenile males spent longer feeding than other members of the population.

As with coprophagy, there was very little difference in the proportion of feeding behaviour comprised by browsing and scratch feeding between the sexes (Figure 6.6). Both sampling methods reflected the similarity of the seasonal pattern between the sexes. Summer months were characterised by the highest levels of non-grazing feeding activity. A decrease followed through autumn months to winter, when the lowest levels of browsing and scratch feeding were seen. Subsequently, an increase through the spring months to the summer high

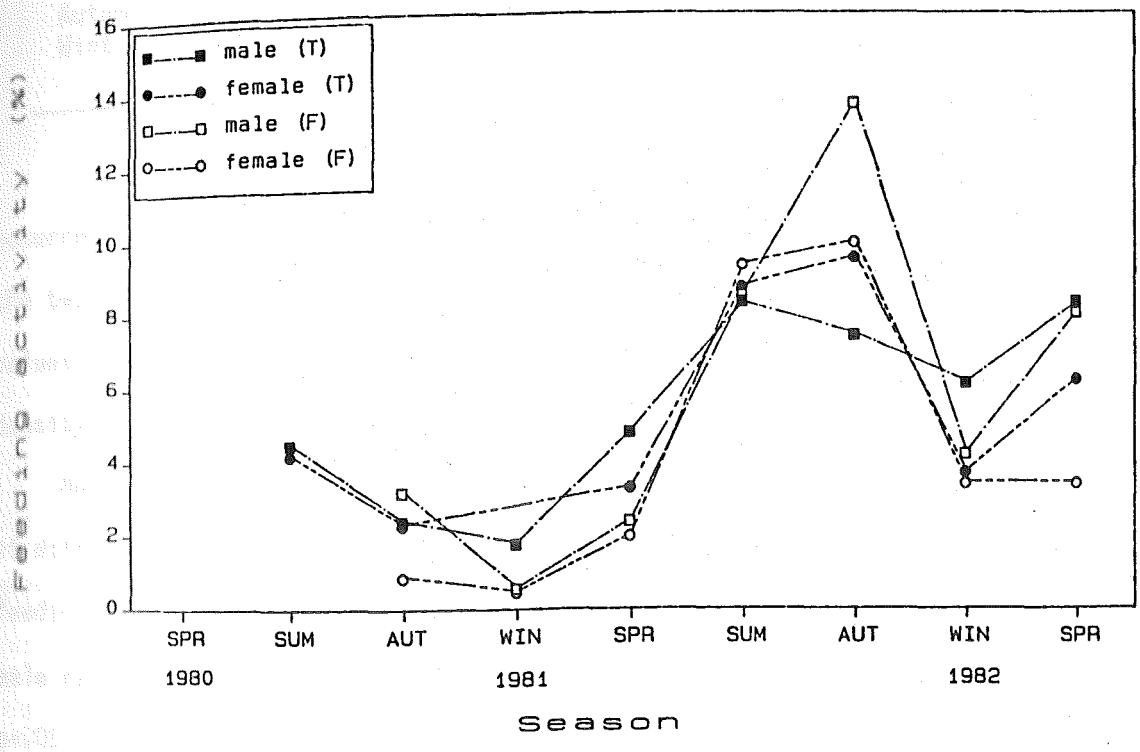


Figure 6.6 Non-grazing feeding activity for male and female rabbits indicated by transect (T) and focal animal (F) sampling.

Table 6.3 Mean seasonal values for transect sampling observations in the feeding category for male and female rabbits.

Season	Percent of observations Males	Females	Difference
Spring	58.6	71.4	12.8
Summer	65.1	67.4	2.3
Autumn	65.1	68.9	3.8
Winter	59.1	62.8	3.9

occurred. Although the overall level of non-grazing feeding differed between the two years of the study, this trend was evident in both years. The higher values in the second year are likely to be related to the higher population density during this period.

Mean seasonal values from focal sampling data were analysed to determine if differences in social status produced variation in the amount of time spent feeding (Table 6.4). The pattern for male rabbits (Figure 6.7a) was clear: male rabbits with a higher social status spent less time feeding ($F=3.59$, $p<.05$), presumably because their superior social status conferred the ability to dominate food resources more effectively than subordinate individuals. The difference between dominant males and males of intermediate and subordinate status was significant (Duncan's new multiple range test, $p<.05$). The difference amongst females of different status (Figure 6.7b) is not as clear: females of intermediate status usually spent the least time feeding while subordinate females spent the most. The difference between these two groups was significant (Duncan's new multiple range test, $p<.05$) although the value for dominant females was not significantly different from either of these two groups.

Feeding behaviour exhibited a steady increase from low levels at midday and in the early afternoon, to a peak around sunset (Figure 6.8). The pattern for all seasons was very similar, the only notable difference being a slightly

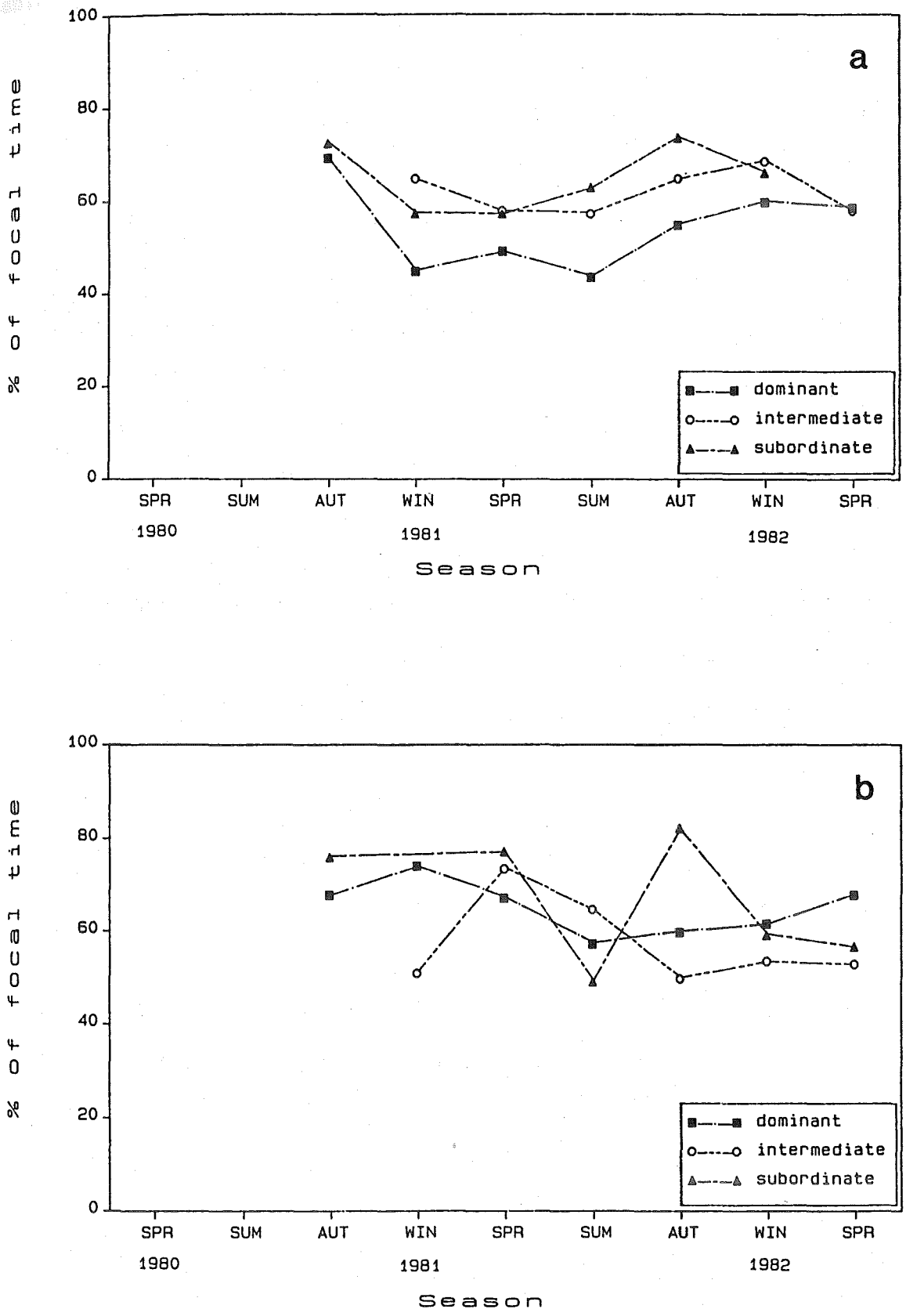


Figure 6.7 Time spent feeding as indicated by focal animal sampling in relation to social status for (a) male and (b) female rabbits.

Table 6.4 Percent of focal sample time spent feeding for rabbits of different social status.

Season	Males			Females		
	Dom	Int	Sub	Dom	Int	Sub
Autumn 1981	69.3		72.5	68.1		76.4
Winter 1981	45.2	64.8	57.5	74.1	51.5	
Spring 1981	49.1	58.1	57.4	67.5	73.9	77.4
Summer 1981/82	43.9	57.5	63.0	57.5	64.7	49.4
Autumn 1982	55.2	64.9	73.9	60.0	50.3	82.4
Winter 1982	60.0	68.8	66.3	61.6	53.7	59.4
Spring 1982	59.0	58.0		68.4	52.9	56.6

Dom = dominant, Int = intermediate, Sub = subordinate

earlier increase in spring compared with winter months. This difference is probably associated with the spring growth phase for most plant species, the need for rabbits to replace fat reserves lost during winter, and in the case of females the increased energy demands of the breeding season. Before studies including nocturnal observations were carried out, rabbits were thought to be primarily crepuscular feeders (Thompson and Worden 1956). However, more recent research has shown that feeding continues throughout the night (Mykytowycz and Rowley 1958, Stodart and Myers 1964, Gibb et al. 1978, Fullagar 1981). Mykytowycz and Rowley (1958) found that the high level of feeding activity reached around sunset is maintained to about midnight, but thereafter declines with feeding activity ceasing completely 2–3 hours after dawn.

6.2.3 Grooming behaviour

The grooming category comprises seven behaviours (viz. scratching, washing, shaking, mutual grooming, stretching, yawning, and rolling). Washing was the most common of these activities, constituting 87% of all grooming behaviour observed during transect sampling. Scratching, shaking, and stretching together made up 12.5% of grooming behaviour, while mutual grooming, yawning, and rolling were rarely seen. In fact, mutual grooming was

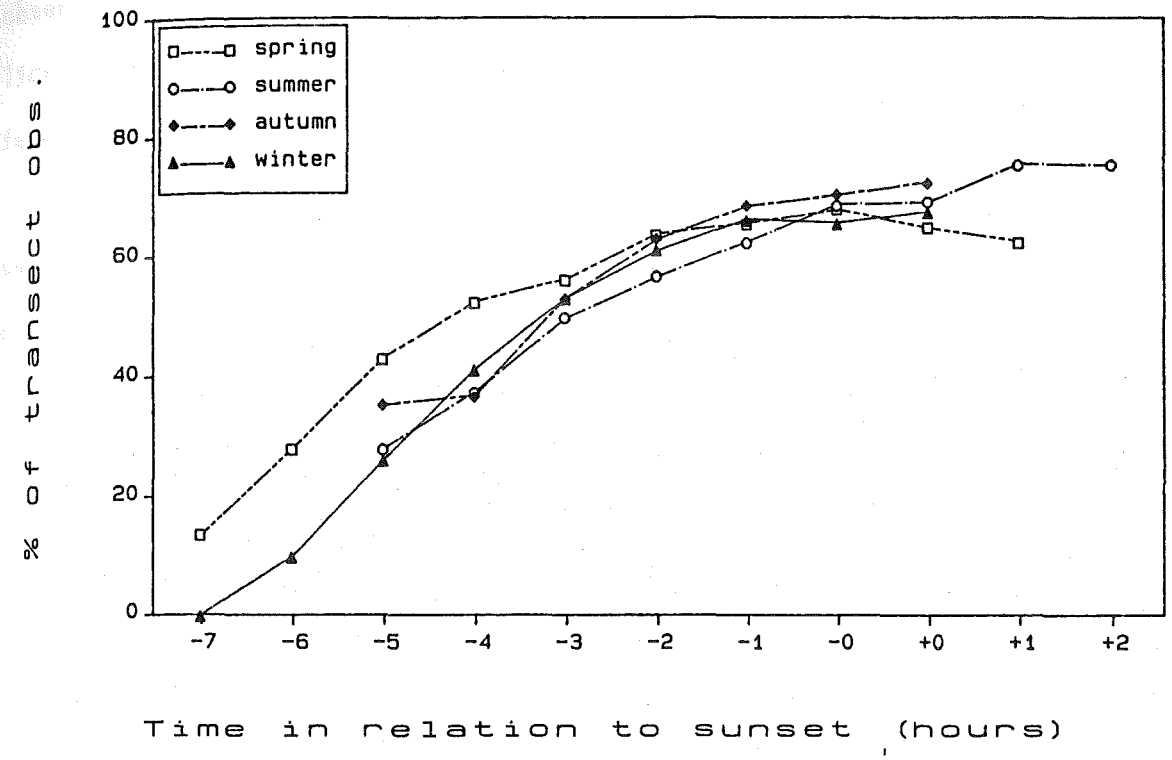


Figure 6.8 Pattern of feeding behaviour in relation to sunset time indicated by transect sampling results pooled by season.

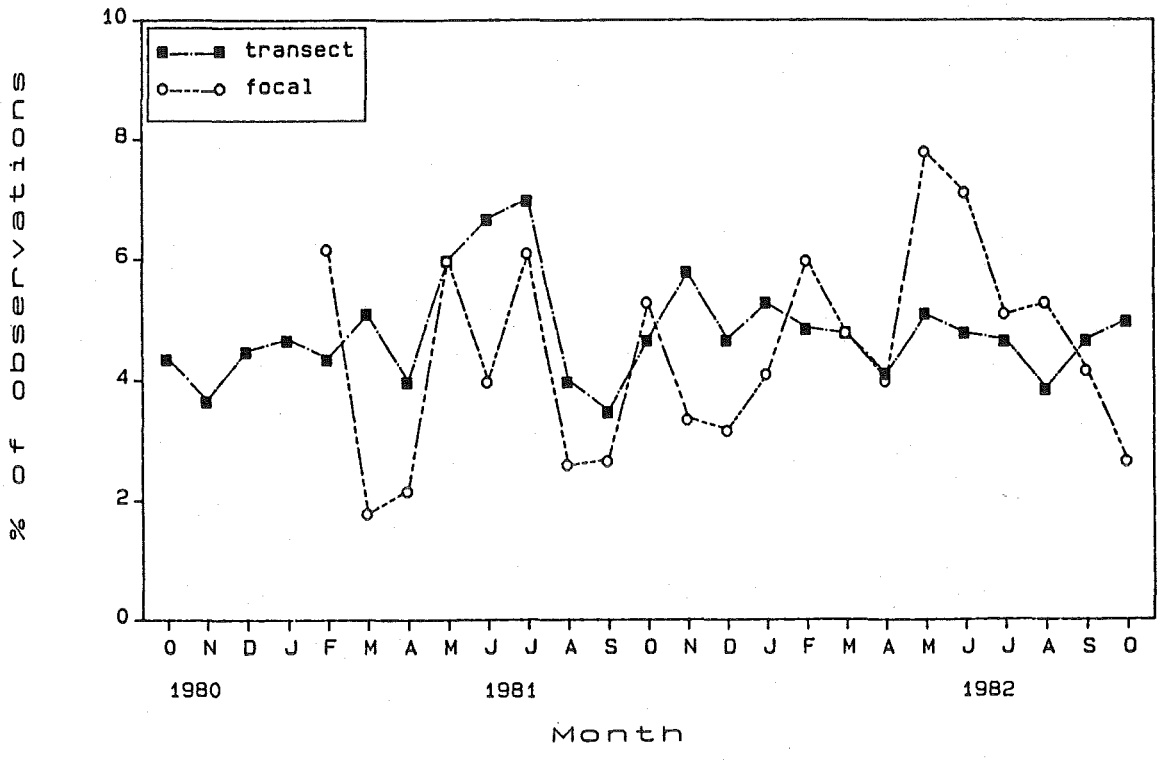


Figure 6.9 Monthly levels of grooming behaviour indicated by transect and focal animal sampling.

observed only once over the entire duration of the study. A male rabbit, M26, licked and nuzzled the head and flanks of an unidentified rabbit, probably a female, for approximately 2 minutes.

Grooming behaviour constituted between 3 and 7% of each month's transect sampling observations (mean=4.8%). Focal sampling produced similar results, although they were somewhat erratic, possibly due to differences in the timing of samples each month (Figure 6.9). Gibb et al. (1978) and Fullagar (1981) found similar levels for grooming behaviour in the period around dusk (ca. 5-7%).

Although the data do not show any definite seasonal pattern, there was a trend towards more grooming behaviour during winter months and less during spring months. Summer and autumn months yielded very similar mean values. The monthly levels for this behaviour category, for both sampling methods, did not exhibit any significant seasonal differences (Duncan's new multiple range test). This lack of variation was not unexpected as the data do not cover the peak period for grooming behaviour (around sunrise, Myers and Poole 1961), when any differences would be expected to occur. Gibb et al. (1978) found that rabbits spent more time grooming in autumn and winter than during spring and summer months. The incidence of grooming behaviour always increased after rain, a feature also recorded by Gibb et al. (1978). A similar effect is produced by the presence of dew (Mykytowycz and Rowley 1958).

The mean levels of grooming behaviour exhibited by the various classes of rabbits, for both sampling methods, are presented in Table 6.5. The most noticeable feature is that the values from focal sampling are consistently lower than those from transect sampling observations. The timing of the samples is probably the factor responsible for this small difference. Transect sampling was favoured in the early afternoon period, in an effort to provide better information on the emergence patterns of the rabbits. Consequently, fewer focal samples were undertaken in the early afternoon. As there was a higher level of grooming activity in the early afternoon (Figure 6.10), focal

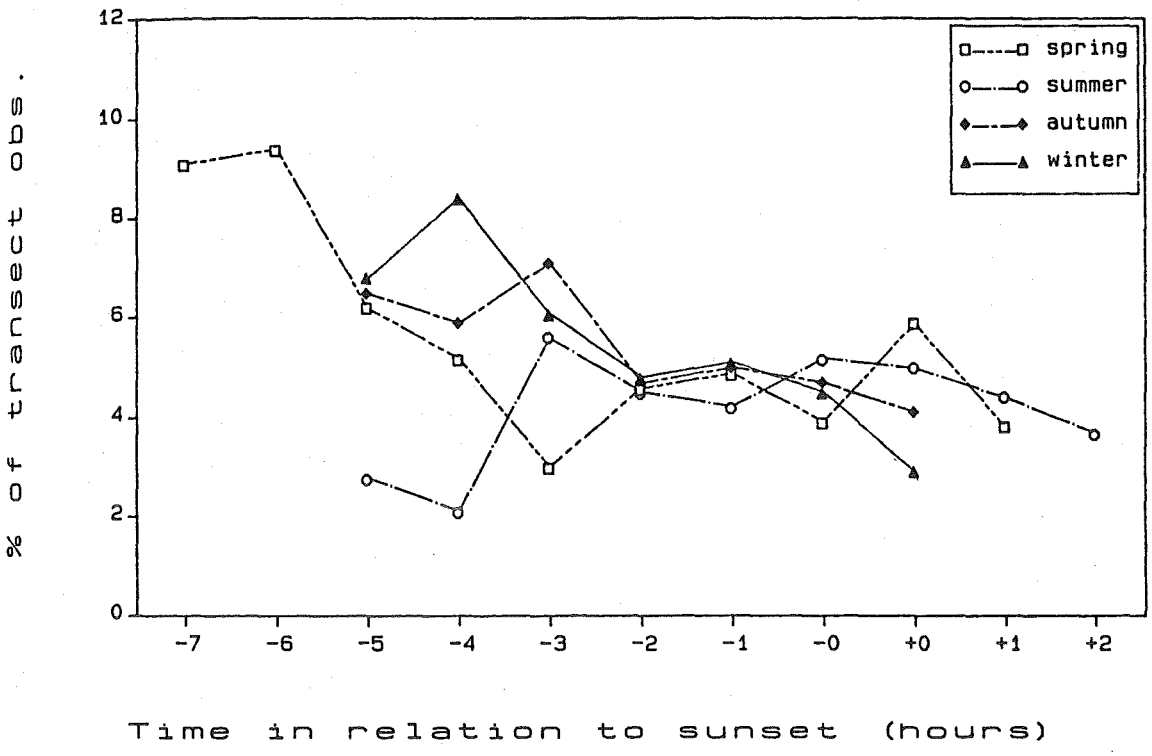


Figure 6.10 Pattern of grooming behaviour in relation to sunset time indicated by transect sampling results pooled by season.

Table 6.5 Mean frequency of occurrence and amount of time spent in grooming behaviour for transect and focal sampling respectively.

Sampling method	Grooming behaviour (%) M	F	U	Y	Total
Transect	5.8	4.4	5.0	3.3	4.8
Focal	5.5	3.9	3.9	3.2	4.5

M = males, F = females, U = unidentified, Y = young

sampling results tend to underestimate the overall incidence of this behaviour category.

The highest levels of grooming activity in most seasons occurred in the period immediately following emergence. The exception to this pattern occurred in summer months, when the level of grooming activities was higher closer to sunset. At this time of year rabbits were often on the surface during most of the daylight hours, although they were usually inactive (i.e. resting). Therefore, a peak in grooming activities may have occurred prior to the start of observations, or the same level of grooming behaviour may have been attained by spreading these activities over a longer period of time. Other studies have found that most grooming behaviour occurs in the early morning following sunrise (Mykytowycz and Rowley 1958, Myers and Poole 1961, Stodart and Myers 1964, Gibb et al. 1978).

Although the mean level of grooming behaviour was lower for female rabbits, for both sampling methods, examination of the transect sampling data showed that this difference was not significant (Wilcoxon signed-ranks test). Young rabbits, however, spent significantly less time grooming than adult rabbits (Wilcoxon signed-ranks test, $p<.01$) as illustrated by results from transect sampling observations for the periods when young rabbits were present (Table 6.6). The values for adult rabbits were calculated by pooling observations for the male, female, and unidentified classes.

Table 6.6 Incidence of grooming behaviour* for young and adult rabbits during transect sampling observations.

Month	Percent of time spent grooming Young	Adult
November 1980	2.3	4.1
December	2.8	5.7
January 1981	4.4	4.8
February	2.1	4.8
October 1981	4.0	4.5
November	3.8	6.8
December	2.7	5.7
January 1982	3.8	5.2
February	4.0	5.8
March	3.7	5.1
April	2.2	4.3

* only data for months when young rabbits were present are included

6.2.4 Resting behaviour

This category consists of four stationary behaviours (viz. sitting, squatting, lying, and basking), which together comprised about 20% of all transect sampling observations. Gibb et al. (1978) found a similar proportion of the Kourarau population resting during dusk observations, but Stodart and Myers (1964) recorded less than 10% of the population they studied resting in the period around dusk. Their results, however, are derived from a small number of observations on an enclosed population that spent most of the daylight hours resting underground. Fullagar (1981) found that within the surface activity period the peak period of resting behaviour occurred in the 2-3 hours before midnight. Sitting and squatting constituted over 90% of all resting behaviour (both for transect and focal sampling), while the lying position accounted for 7-9% and basking less than 1%.

There was a marked difference in the amount of resting behaviour between the two sampling methods, with a tendency for focal samples to reflect a higher incidence of resting behaviour. This is mainly because stationary

rabbits were chosen for focal sampling more frequently than active ones, as tag identification was much easier. If those focal samples which began with resting behaviour are removed from the data set, a pattern much closer to that for transect sampling is produced. Nevertheless, the relative trends within both types of data, not only for the category overall but also for individual behaviours within the category and for the various segments of the population, are similar even though the absolute values are not.

Although a seasonal pattern for the resting category overall is not well defined, a trend is evident if the transect sampling data are examined closely. There appears to be an increase in the amount of time spent resting in winter and summer months from the lower levels maintained during autumn and spring months. On cold winter days most resting rabbits chose a sheltered position, usually in the lee of rocks or thyme bushes, especially if the low temperatures were accompanied by southerly winds or heavy rain. Gibb et al. (1978) also noted that rabbits sheltered from these weather conditions. Similarly, on hot summer days rabbits sought out patches of shade in which to sit or squat.

Throughout the year sitting and squatting comprise the majority of resting behaviour, whereas lying and basking are strictly seasonal in their occurrence (Figure 6.11). The latter two activities were most common during the warmest months of the year (late spring, summer and early autumn), but almost completely absent during winter. The low values recorded for lying and basking in January and December 1981 were also seen for sitting and squatting. Weather conditions observed during the sample times were typical for these months and cannot be used to account for the difference in the amount of resting behaviour compared with the surrounding months. However, in both cases the rainfall for the previous three months was only 70% of the usual amount. This probably resulted in reduced plant growth causing rabbits to spend more time foraging for food. In fact, such an increase in feeding activities was observed during these two months (see Figure 6.3), confirming the relationship

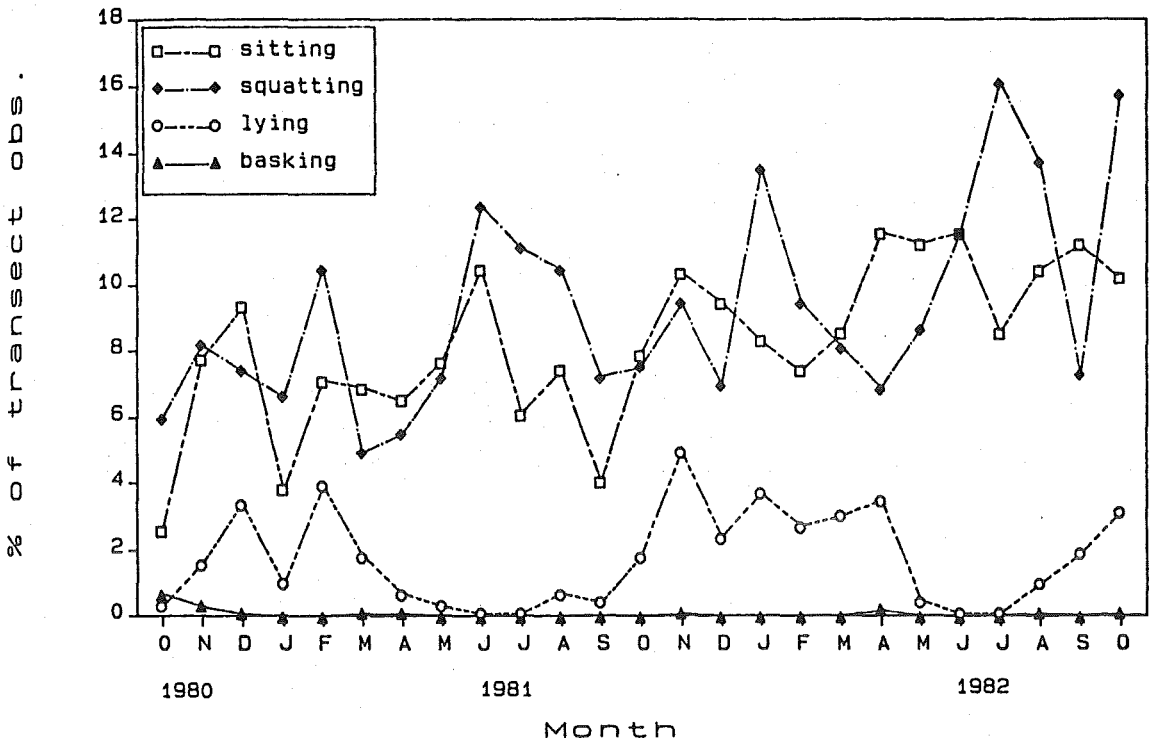


Figure 6.11 Monthly levels of each activity within the resting behaviour category.

between feeding and resting behaviour (Gibb et al. 1978). A similar effect has been reported in relation to population density and its effects on the food supply (Myers and Poole 1961, 1962).

The high incidence of sitting and squatting all year round reflects the prevalence of these two postures when rabbits are inactive. Conversely, lying and basking are the result of not only inactivity but also specific weather conditions. These two activities were influenced most by temperature (Figure 6.12a). The frequency of lying and basking each month was significantly correlated with the average maximum temperature for that month ($r=0.71$, $p<.001$). The strong relationship between these two activities and temperature was confirmed by individual monthly data. Within a particular month's behaviour observations the frequency of lying and basking were related to individual daily temperatures. The trend was towards a higher frequency of these activities on warmer days as the data for four consecutive days in December 1981 show (Figure 6.12b). Weather conditions over this period were generally similar with the exception of the variation in temperature.

The amount of resting behaviour observed was related to the time of day (Figure 6.13). From a peak around the midday-early afternoon period, the proportion of resting behaviour declined steadily with the lowest levels around or slightly after sunset.

Male and female rabbits spent similar amounts of time in resting behaviours, although there was a general trend for males to spend slightly more time resting in the first year of the study. In the second year of the study this pattern was reversed with females spending slightly more time resting. Transect data for the period December 1980-December 1981 indicate a significant difference (Wilcoxon signed-ranks test, $p<.01$) in favour of more resting behaviour for males, while the difference for the period January 1982-August 1982 was also significant (Wilcoxon signed-ranks test, $p<.05$), this time in favour of females.

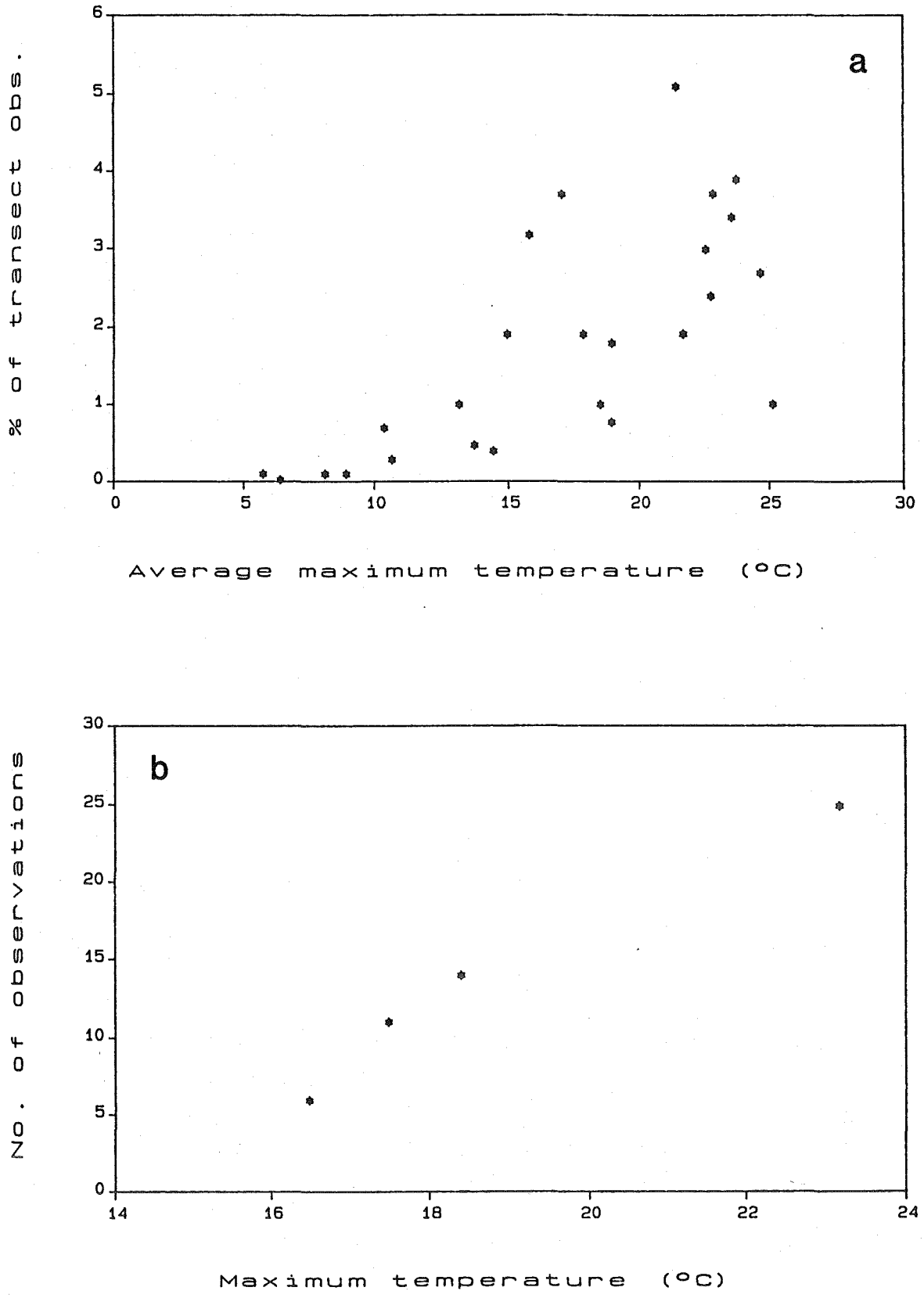


Figure 6.12 Frequency of lying and basking behaviour in relation to (a) the average maximum temperature each month and (b) the maximum temperature on four consecutive days in December 1981.

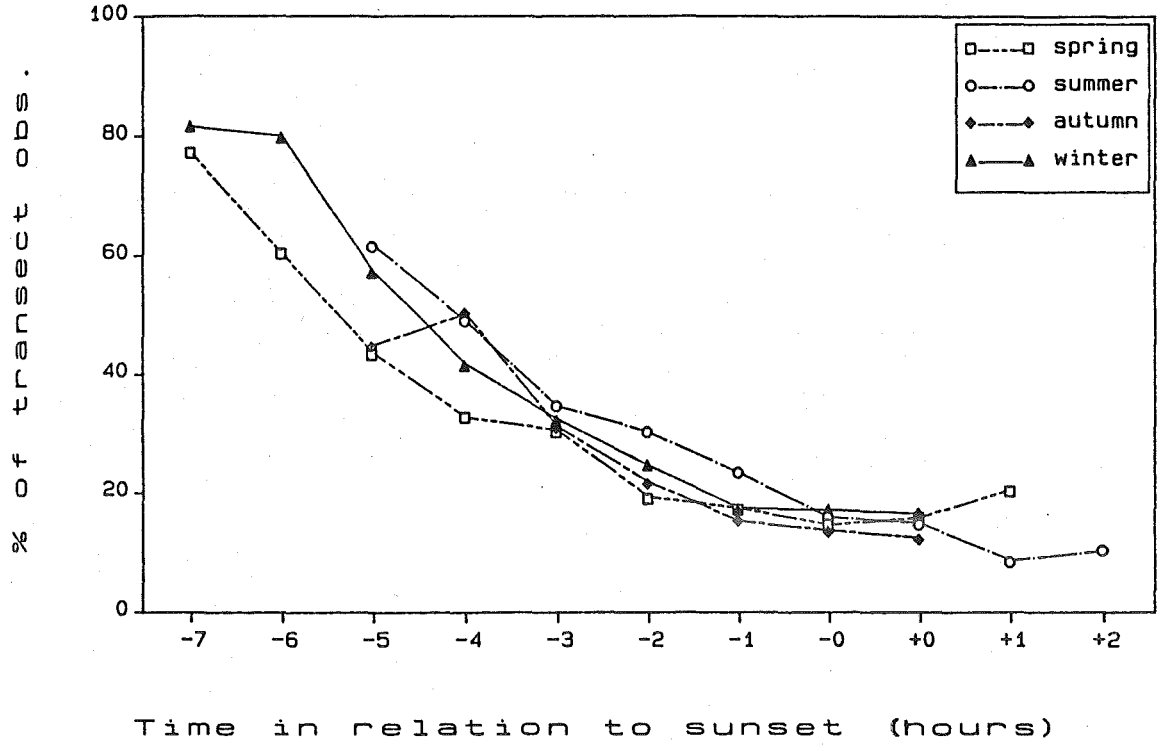


Figure 6.13 Pattern of resting behaviour in relation to sunset time indicated by transect sampling results pooled by season.

There was a considerable difference in the amount of resting behaviour between young and adult rabbits. During the early part of the breeding season (September-November) young rabbits spent approximately 30% of their time resting, considerably more than adult rabbits during the same period (less than 20%). However, in the following months this comparatively high incidence of resting behaviour decreased until young spent a similar amount (as in January-March 1981) or less time (as in January-March 1982) resting than adults. This trend for young rabbits was most closely associated with the change in the amount of time spent feeding (see section 6.2.2).

6.2.5 Locomotory behaviour

There were only three behaviours in this category (viz. lope, run, and skit). Loping was the most common, comprising over 90% of all locomotory behaviour observed in both types of sampling. The two other locomotory activities, run and skit, comprised approximately 6% and 3% of the locomotory category respectively (transect sampling data). Movements were also associated with other forms of behaviour, including activities within the feeding, reproductive, territorial, and aggressive categories. However, apart from the skit behaviour which could not be associated with any other category, all the locomotory observations included in these results involve movements that were not associated with any other behaviour category.

Locomotory activities constituted between 4 and 10% of transect sampling observations, whereas focal sampling revealed a much lower level for this category (less than 3% of focal sample time). Although behaviour observations represent only a particular period of activity (i.e. afternoon and early evening), they are similar to levels of locomotory activity found by Gibb et al. (1978) (1.3-4.0%) and Fullagar (1981) (3.9-4.9%). Fullagar's observations covered the complete 24-hour period. The higher levels recorded in this study during transect sampling (which was comparable to their methods of observation) may represent a period when the level of locomotory behaviour is

greater than the daily average. This is confirmed to some extent by information given below on changes in the level of locomotory activity in relation to time. Fullagar (1981) found that the peak of locomotory activity (12-13% of total observation time) occurred during the period between sunset and midnight.

The most noticeable feature from the monthly data was the decline which occurred in the amount of locomotory activity around August 1981. This decline was evident in both transect and focal sampling data and could have been associated with the higher population density in the second year of the study (see section 9.2.5). Gibb et al. (1978) recorded a similar decrease in the amount of locomotory activity as population density increased.

There did not appear to be any seasonal pattern in the incidence of overall locomotory behaviour. However, this is largely because of the prevalence of the loping activity. The two less frequent activities, run and skit, were highly seasonal in their occurrence (Figure 6.14), but because of their relatively low frequencies compared to loping did not influence the overall pattern enough to confer seasonality. Both were more frequent in spring and summer and nearly absent in autumn and winter. The factor most responsible for this effect was the presence of young in the population because most occurrences of these two activities were due to young rabbits (Table 6.7). Despite the fact that over the duration of the study less than 12% of all transect sampling observations were on young rabbits, they accounted for 54% and 83% of observations in the run and skit categories respectively.

The skit behaviour is highly characteristic of young rabbits and involves rapid, erratic movements often including leaping and somersaulting in the air. Such behaviour is usually of short duration (10 seconds or less) and occurs close to the burrow or breeding stop. On a number of occasions skit behaviour by one young rabbit precipitated similar activity in one or more of its litter mates. The incidence of this behaviour is highest in recently emerged young,

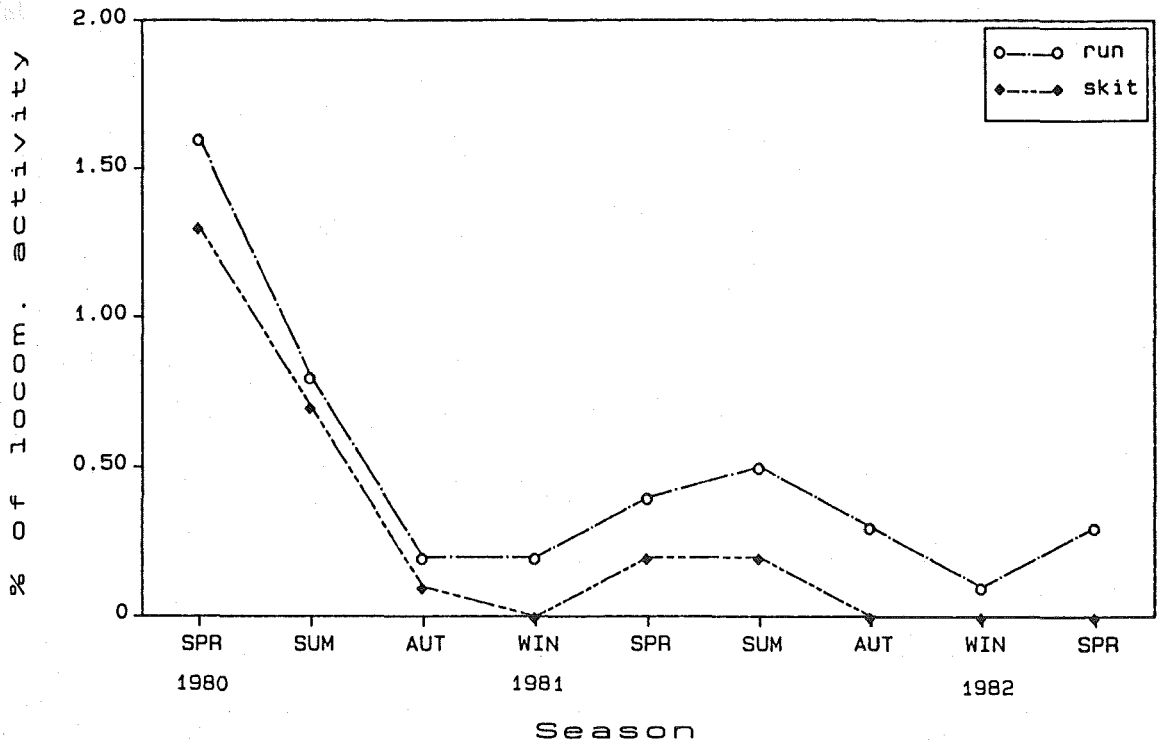


Figure 6.14 Frequency of the run and skit activities within the locomotory category indicated by transect sampling results pooled by season.

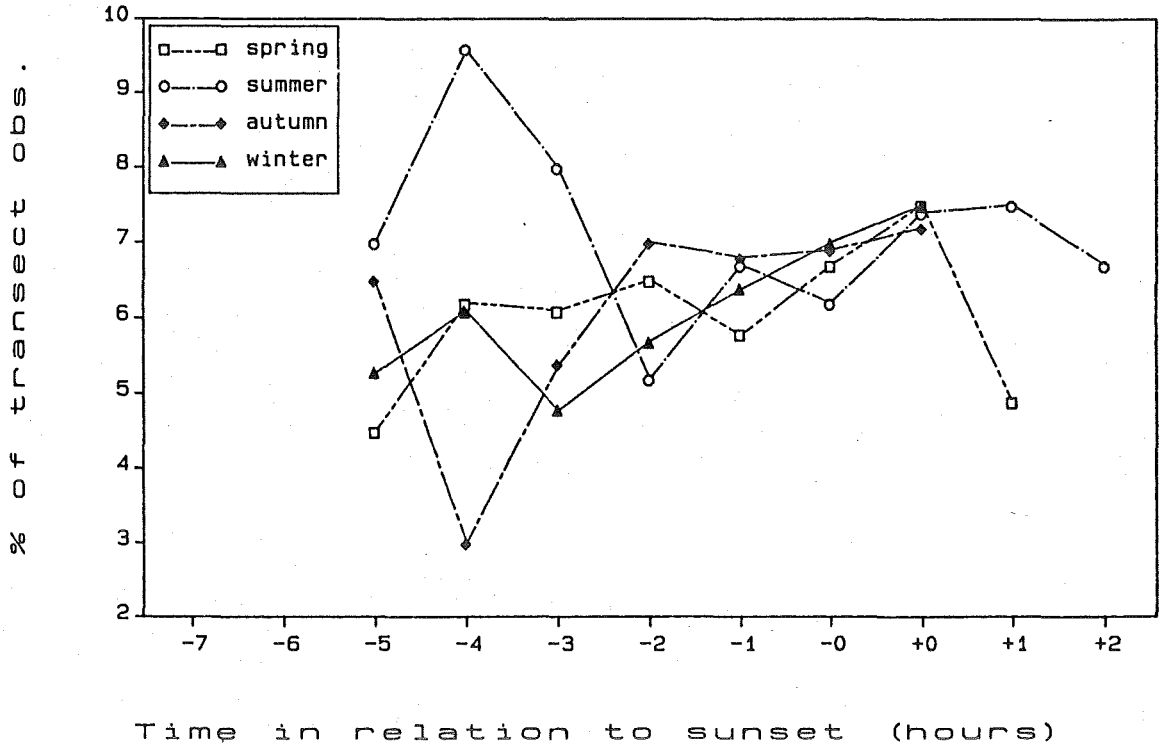


Figure 6.15 Pattern of locomotory behaviour in relation to sunset time indicated by transect sampling results pooled by season.

Table 6.7 Percent occurrence for adult (A) and young (Y) rabbits of the three locomotory activities, pooled by season (transect data).

Season	Lope n	Lope A	Lope Y	Run n	Run A	Run Y	Skit n	Skit A	Skit Y
Spring	(760)	82	18	(75)	32	68	(46)	17	83
Summer	(821)	61	39	(77)	34	66	(49)	10	90
Autumn	(695)	97	3	(22)	95	5	(3)	67	33
Winter	(766)	100	0	(16)	100	0	(2)	100	0
Total	(3042)	84	16	(190)	46	54	(100)	17	83

n = number of observations

during their first few weeks above ground, and subsequently declines with age.

The incidence of locomotory behaviour in transect sampling observations was significantly higher for male rabbits compared with females (paired t-test, $t=2.81$, $p<.05$). Although focal samples exhibited the same trend, with males spending more focal sampling time engaged in locomotory activity, the difference was not as great ($t=1.34$, NS). This may have been due to a slightly smaller data set for the focal samples, or it could have arisen because although female rabbits had a lower frequency of occurrence for locomotory activities the durations were greater than for male rabbits.

A similar relationship existed between young and adult rabbits, with more locomotory activity attributed to young rabbits by both sampling methods. However, whereas this difference was significant for transect sampling observations ($t=3.60$, $p<.01$), it was not for focal sampling observations ($t=1.29$, NS).

Throughout the observation period there was little diurnal change in the level of locomotory behaviour except for a gradual increase towards sunset (Figure 6.15). The pattern was similar in all seasons, although during summer months the level of locomotory activity was quite high in the early afternoon. A greater proportion of the population was active on the surface at this time of year, which may have influenced the amount of locomotory behaviour.

6.2.6 Alert behaviour

There were four activities classified in this category (viz. upright, crouch, thump, and fleeing), all of which are displayed in the context of danger or nervousness on the part of the individual. The first two, upright and crouching, are postures adopted when the rabbit senses danger. These postures are characterised by the head and body orientated towards the sound or movement, with ears forward and nose raised, and with visible sniffing behaviour. The upright stance is used also by rabbits exploring areas outside their normal ranges. In these situations they appear nervous and frequently assume an upright posture to survey their surroundings. Thumping and fleeing are direct consequences of a rabbit detecting a definite danger. In most instances an adult rabbit will thump one or more times before fleeing, and this acts as a warning signal to other rabbits in the vicinity.

Several interesting facets of behaviour were noted for activities within this category. Often a rabbit in the crouch position would raise and lower its head and the anterior part of its body by flexing and stretching its forelegs and neck. The result was a very characteristic action best described as 'head-bobbing'. Such activity was most common in rabbits exploring areas outside the range of their normal movements, and generally indicated a high level of alertness.

Another intriguing occurrence was that of the thump behaviour in an aggressive context. On one occasion two females, F02 and F51, thumped several times over a period of four minutes. Unlike typical instances of thumping behaviour, other rabbits in the vicinity appeared unaffected, suggesting that on this occasion the activity was not a sign of danger but rather some form of interaction between the two females. This incident occurred in June 1981, a time when social group formation prior to the breeding season caused increased levels of aggression between rabbits as they reestablished their positions in the dominance hierarchy. At this time F02 was dominant and F51 was intermediate in social status although several months later, following the

disappearance of F02, F51 established herself as the dominant female in the social group. During an experimental study of aggressive behaviour in captive rabbits, Mykytowycz and Hesterman (1975) also recorded instances of thumping in an aggressive context.

Unlike the incident of aggressive thumping described above, most alert behaviour by one rabbit would precipitate similar activity by other rabbits, confirming the warning signal function of these behaviours, especially thumping and fleeing. Fleeing was distinctive from other forms of locomotion, not only in the speed at which it occurred but also in the position of the tail. Loping and running rabbits were characterised by a relaxed tail, held almost horizontal to the ground. In contrast, fleeing rabbits held their tails erect so that their rapid running motion caused the white underside to flash repeatedly, a very strong visual warning signal to other rabbits.

Although alert behaviours were not uncommon, overall they formed only a small proportion of each month's total number of transect sampling observations (mean=1.2%). Similarly, for focal sampling they represented only 0.2-1.2% of the total sample time each month (mean=0.8%). These values correspond closely to those of 0.6% and 0.9% for two rabbit populations studied by Fullagar (1981). There was no clear seasonal pattern to the incidence of alert behaviour, possibly a reflection of a complex of factors influencing this category. However, one trend is apparent, that of a decline in the proportion of alert behaviour over the duration of the study (Figure 6.16). The best illustration of this trend is given by a comparison of the transect sampling data for the period January-October in 1981 with the same period in 1982 (Table 6.8). The amount of alert behaviour was significantly greater in 1981 than in 1982 (Wilcoxon signed-ranks test, $p<.01$). Interestingly, the population density in 1982 was higher. The number of hawk sightings was relatively similar in both years (see Figure 9.9), implying a lowered risk of predation in 1982 and a greater ability of the population to detect danger. These factors may account for the noticeable decrease in time

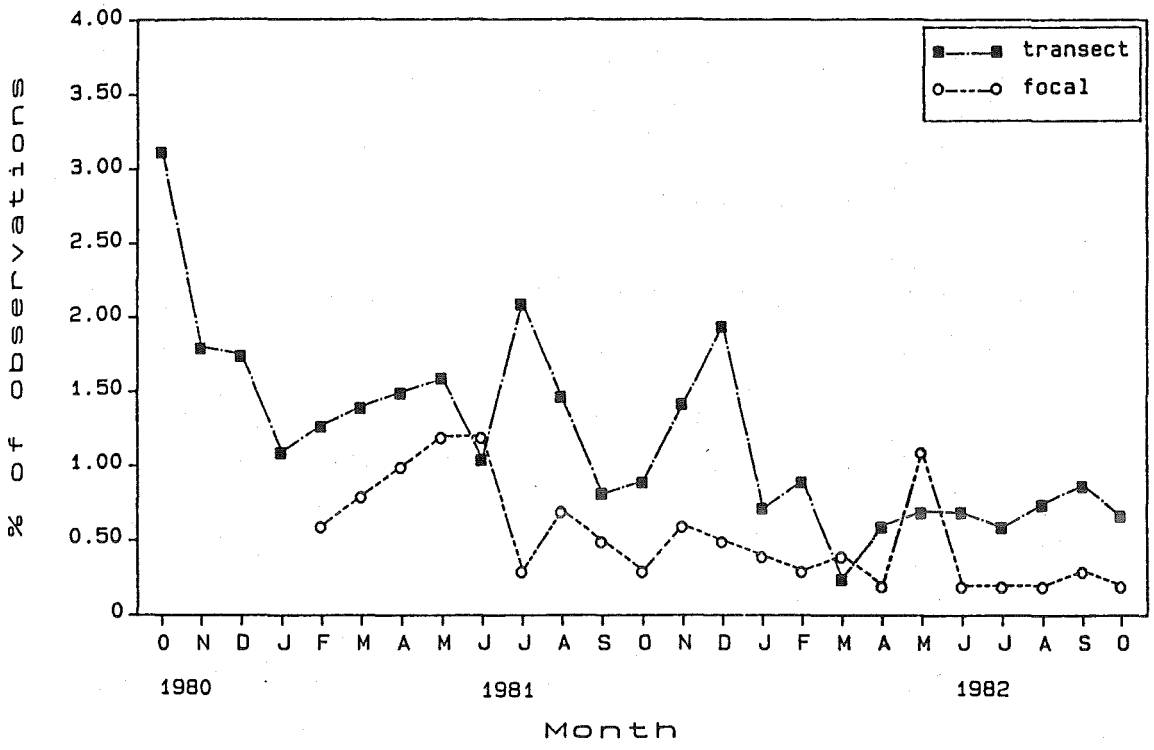


Figure 6.16 Monthly levels of alert behaviour indicated by transect and focal animal sampling.

Table 6.8 Percent of transect sampling observations comprised by alert behaviours for the period January-October in 1981 and 1982.

Month	Percent of transect observations 1981	1982
January	1.10	0.72
February	1.28	0.90
March	1.40	0.25
April	1.51	0.61
May	1.59	0.70
June	1.06	0.69
July	2.10	0.59
August	1.47	0.75
September	0.82	0.88
October	0.90	0.67

spent in alert behaviours between the two years.

The amount of focal sample time spent in alert activities was similar for male (0.6%) and female rabbits (0.8%). This is supported by the frequency of occurrence data from transect sampling where the incidence of alert activities was 0.8% for males and 0.9% for females. Young rabbits spent more time alert than adults (1.5% of transect sampling observations, cf. 1.1% for adults). This difference is confirmed by the results from focal sampling for the period October 1981 to April 1982 (Table 6.9). The comparison is restricted to these months because, with the exception of one sample in October 1982, this was the only time that focal samples were recorded for young rabbits. As Dunnet (1957b) noted, young rabbits were noticeably more susceptible to disturbances, not only by potential predators but also by factors such as gusts of wind and the movements of other rabbits (see Figure 5.2). Hawks tended to concentrate their predatory activities on young rabbits. During observations, several young were killed by hawks over the duration of the study compared with only one adult rabbit.

Table 6.9 Percent of focal sampling time spent in alert behaviour by young and adult rabbits between October 1981 and April 1982.

Month	Percent of focal time Young (n)	Adult (n)
October 1981	0.0 (2)	0.2 (40)
November	0.8 (22)	0.3 (20)
December	0.3 (37)	0.1 (16)
January 1982	0.3 (16)	0.1 (35)
February	0.9 (17)	0.4 (28)
March	0.0 (2)	0.2 (30)
April	0.0 (1)	0.0 (6)

n = number of focal animal samples

6.2.7 Reproductive behaviour

This category contained the largest number of different behaviours. Thirteen activities were recognised (viz. inspecting and inspected, following and followed, circling and circled, enurinating and enurinated, nuzzling and nuzzled, copulation attempt, mounted, and copulating). Similar activities have been reported for two North American lagomorphs, the cottontail and the swamp rabbit **Sylvilagus aquaticus** (Marsden and Holler 1964). Reproductive behaviours are dyadic activities, where two rabbits participate in a particular behaviour or behaviour sequence. The male usually engages in the more active behaviour while the female may be either passive, simply the target of the male's activity as in 'enurinated', or active as in 'followed' where the movements and changes of direction by the male are influenced by those of the female. A related activity, nursing behaviour by female rabbits, takes place within the breeding stops during the hours of darkness and was therefore impossible to observe. However, it is of very short duration with the female suckling the young only once every 24 hours and then for only several minutes (Duestch 1957, Mykytowycz and Rowley 1958). Similar behaviour has been reported among other lagomorphs (see Broekhuizen and Mulder 1983).

Although reproductive behaviours are very important in the life history of the rabbit, they comprised less than 1% both of transect and focal sampling observations. Nevertheless, the data provide a useful picture of the breeding activities within the population throughout the year. Although transect and focal sampling methods produced different results in terms of the overall levels of reproductive behaviour observed, trends within the data from the two sampling methods were very similar. The number of observations of reproductive behaviour for male and female rabbits were almost identical. Neither sampling method produced any observations of young rabbits engaged in reproductive activities. However, in the later months of the breeding season it was not uncommon to see rabbits of intermediate age (i.e. subadults) engaged in 'following'. This is the most general of all the reproductive activities, functioning mainly as a preliminary to more specific reproductive behaviour. Southern (1948) noted that rabbits of about 16 weeks old exhibited rudimentary forms of reproductive behaviour.

The highest incidence of reproductive behaviour occurred immediately before and during the initial stages of the breeding season (late winter and spring months) when it comprised 1-2% of transect sampling observations. The monthly frequency of occurrence data from transect sampling were tested for seasonal variation using an ANOVA. While a significant result ($F=6.7, p<.05$) was revealed using the traditional seasonal groupings, an increase in significance was produced when data for August were lumped with the spring months ($F=15.8, p<.001$). The level of reproductive behaviour for the months August-November inclusive was significantly greater than at other times of the year (Duncan's new multiple range test, $p<.01$).

Reproductive activities were noted in all seasons (see Figure 6.17), although during the non-breeding period the range of reproductive activities was restricted (Table 6.10). At these times inspecting or following were the most common activities noted and could possibly have been in the context of some other behaviour sequence rather than a reproductive one. Within the

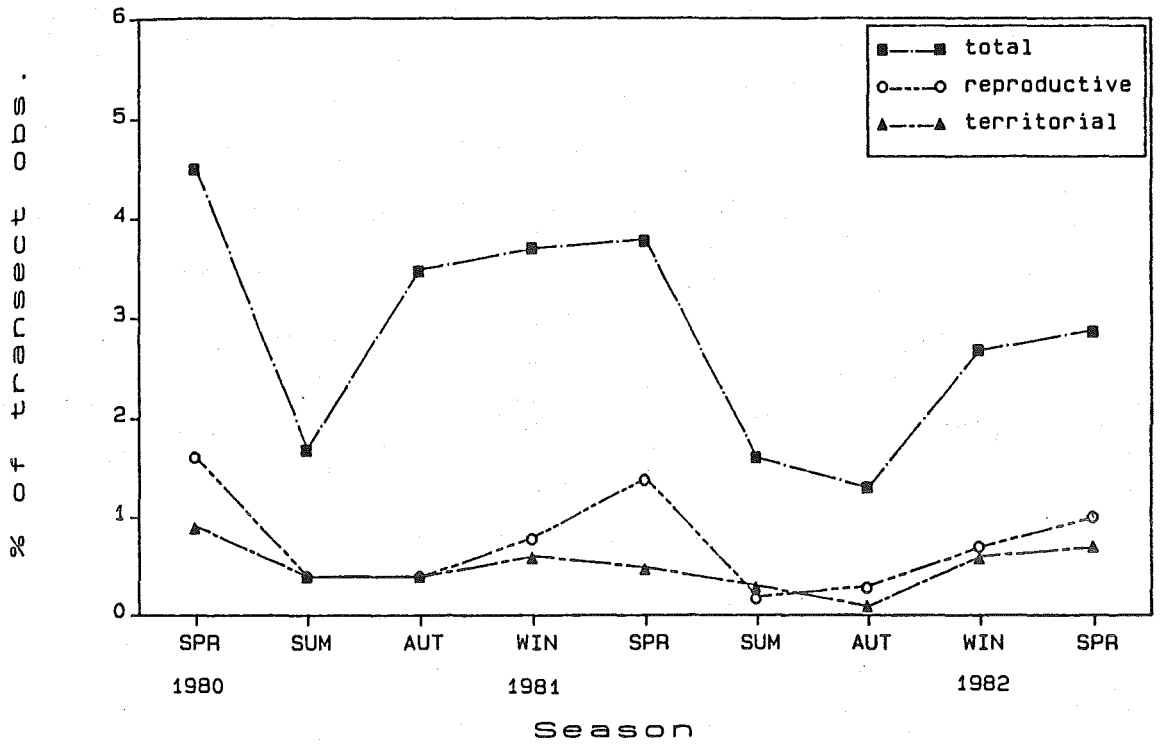


Figure 6.17 Frequency of reproductive, territorial, and total social behaviour (includes aggressive and displacement) indicated by transect sampling results pooled by season.

breeding season, behaviours more closely associated with reproduction (circling, enurination, nuzzling, and copulation) were observed, whereas these were almost completely absent at other times of the year. Of the eight occurrences of circling noted in autumn 1981, six were in May, suggesting a slightly earlier than usual start to breeding activities by some individuals in 1981.

If 'inspection' is excluded, there is an interesting trend in the frequency of reproductive behaviours (see Table 6.10) with the most general activities being commonest, the frequency declining as the activities become closer to the ultimate reproductive behaviour, copulation. A similar pattern emerged from Southern's (1948) observations. This verifies that there is a definite overall sequence of reproductive behaviours. Although it was rare to observe a complete sequence of behaviours, copulation attempts were always preceded by one or more other reproductive behaviours. The preliminary reproductive behaviours function to synchronise the activities of male and female rabbits, and to enable the male to gauge the receptivity of the female.

Table 6.10 Occurrences of reproductive behaviour groupings from transect sampling observations, pooled by season.

Season	Behaviour groupings 36/37	38/39	40/41	42/42	44/45	47-49
Spring 1980	2	64	10			
Summer 1980/81	1	18				
Autumn 1981	5	4	8	2		
Winter 1981	2	20	6	3	4	3
Spring 1981	2	55	14	6	4	4
Summer 1981/82	4	10				
Autumn 1982	8	4				
Winter 1982	2	44	2	2	2	
Spring 1982	4	24	2	2		
Frequency (%)	8.7	70.0	12.1	4.3	2.9	2.0

36 = inspects, 37 = inspected, 38 = following, 39 = followed,
40 = circling, 41 = circled, 42 = enurinates, 43 = enurinated,
44 = nuzzles, 45 = nuzzled, 47 = copulation attempt, 48 = mounted,
49 = copulates

Following and circling activities by male rabbits elicited a variety of responses from female rabbits. If the female was not receptive she ignored the attentions of the male, usually by feeding in a desultory manner. Sometimes when a non-receptive female was the subject of persistent circling by a male rabbit, she would continually reorientate towards the male thereby denying him access to her flanks or hindquarters. In a few cases the male's persistent behaviour elicited an aggressive response, usually taking the form of a threat by the female. Almost invariably this caused the male to cease and retreat, sometimes followed by some form of displacement activity. A considerable number of reproductive advances by male rabbits were repulsed by females, as observed in other studies (Southern 1948, Mykytowycz and Rowley 1958).

Enurination was the reproductive activity most frequently seen in an aggressive context, a feature also noted by Southern (1948). Although it was most commonly reproductive and involved a male rabbit enurinating a female, instances of female rabbits enurinating other females or male rabbits were observed. No definite observations of male rabbits enurinating other males were recorded, although this has been reported previously (Southern 1948, Lockley 1961). The response of female rabbits to enurination varied from indifference to mild disturbance, usually leading to shaking and grooming. Enurination did not appear to directly precipitate further reproductive behaviour. Its primary function is to mark the female with odours from the male's urine, especially around the time when the female is in oestrus (Marsden and Holler 1964).

When the data were examined with respect to social status, significant differences were found in the number of reproductive acts engaged in by rabbits of different status (Table 6.11). The difference among males of different social status was highly significant (chi-square=43.4, $p<.001$); a significant difference existed for females also (chi-square=13.0, $p<.01$). Each social status level for males was significantly different from the others at the 1% level, whereas for females no significant difference was evident

Table 6.11 Number of reproductive acts observed for male and female rabbits of different social status.

Sampling method	Males			Females		
	Dom	Int	Sub	Dom	Int	Sub
Transect sampling	26	17	10	13	17	10
Focal sampling	71	34	17	32	41	15
Total	97	51	27	45	58	25

Dom = dominant, Int = intermediate, Sub = subordinate

between individuals of dominant and intermediate status. However, both these groups were significantly different from subordinate females at the 5% level. Similar patterns caused by social status differences have been reported elsewhere (Southern 1948, Mykytowycz 1959, 1961).

During the non-breeding season, behaviours within the reproductive category were not concentrated within any particular period, lending weight to the suggestion that they may have occurred in the context of some other activity. However, during the breeding season there was an increase in the incidence of reproductive activities after sunset. This pattern has been reported previously (Rowley and Mollison 1955, Myers and Poole 1962, Stodart and Myers 1964, Fullagar 1981).

6.2.8 Territorial behaviour

Only three behaviours comprised this category (viz. tail-flagging, chinning, and patrolling). As with the other social behaviour categories, territorial behaviour comprised very few of the observations for both transect (0.44%) and focal sampling (0.18%). Tail-flagging (47%) and chinning (41%) formed the majority of territorial behaviour observed, with patrolling (12%) recorded less frequently, partly because it was difficult to identify.

Tail-flagging has previously been included in the reproductive category by Southern (1948) and others. However, observations during this study indicated that it was better placed with the territorial behaviours. Generally, it was an intrasexual display characterised by extremely exaggerated movements. The posture adopted made maximum use of the strong visual signal of the tail's white underside, and frequently tail-flagging progressed to another form of territorial behaviour (chinning) or displacement behaviour. In some cases tail-flagging led to fighting or chases. The placement of tail-flagging in the reproductive category in other studies may be due to the similarity of the gait involved. The tail is held erect by male rabbits during the reproductive following and circling behaviours, although the movements are stiffer and more exaggerated when this posture is associated with territorial display.

Chinning occurs so that secretions from the superficial sub-mandibulary (chin) glands are deposited on objects within the rabbits home range (Mykytowycz 1964). Frequently chinned objects included rocks, dead vegetation, the ground, and sometimes other rabbits. Chinning activity was especially common around burrow entrances.

Patrolling was a particularly difficult behaviour to identify and as the experience of the observer increased towards the end of the study, the number of observations attributed to this behaviour decreased as activities similar to patrolling (and probably recorded as such earlier in the study) were placed in their correct category.

Because the number of observations within the territorial category was so low, it was not possible to examine the monthly data separately. Consequently, seasonal groupings have been used for all analyses. Transect sampling observations showed that the overall population levels of territorial behaviour were highest during winter and spring months and lowest during summer and autumn (see Figure 6.17). Other studies suggest that outside the breeding season territorial behaviour is seldom seen (Lockley 1961, Mykytowycz

1964). However, this is a very generalised view and does not highlight the marked differences that occurred between different segments of the population.

Only adult rabbits engaged in territorial activities. In over 5000 separate observations during transect sampling, young rabbits were never observed engaging in territorial activities. Myers and Mykytowycz (1958) found that subordinate females, as well as young rabbits, took no part in territorial defense.

There was a marked difference in the level of territorial behaviour between male and female rabbits in all seasons and for both sampling methods. Almost 90% of territorial observations on marked rabbits were on males, a highly significant result (paired t-test, $t=4.86$, $p<.001$). The pattern was similar for each of the territorial activities, with male rabbits accounting for 87% of tail-flagging observations, 90% of chinning observations and 71% of patrolling observations. The lower value recorded for patrolling may be due to the small number of observations of this behaviour ($n=14$).

The greater involvement of male rabbits in territorial behaviour has been well established by many previous behavioural studies (e.g. Southern 1948, Lockley 1961, Myers and Schneider 1964, Mykytowycz 1964). Studies on the odoriferous glands of rabbits (Mykytowycz 1962, 1967, Mykytowycz and Dudzinski 1966) show there is a pronounced sexual dimorphism in the size of these glands. Measurements taken from rabbits killed during the control operation confirmed this variation (see section 7.2.4). A marked difference exists in the size of the chin glands between rabbits and hares (Mykytowycz 1965, 1967). The chin glands of female hares are approximately half the weight of those of female rabbits, despite the fact that hares weigh roughly twice as much as rabbits. The difference is even more pronounced amongst males; the chin glands of male rabbits are approximately four times larger than those of male hares. These differences are associated with the wider-ranging movements of the hares in comparison to the strongly territorial, gregarious nature of rabbit populations. In addition to size differences, the secretory activity of the

odoriferous glands is directly related to the territorial activities of the individual (Mykytowycz and Dudzinski 1966).

Examining the data pooled by season, there appears to be very little pattern in the distribution of territorial behaviour with time of day. The most noticeable feature is the seasonal variation. However, if the data from all seasons are pooled some trends are evident. Territorial behaviour tends to increase and reach its highest levels 2-3 hours before sunset, and thereafter it declines gradually. The peak period corresponds to a time when most emergence is occurring and presumably rabbits are emphasizing (tail-flagging and patrolling) and re-marking (chinning) territorial borders and objects within their range.

Social status was strongly correlated with the amount of territorial behaviour an individual engaged in, for both males and females (Table 6.12). Male rabbits of higher social status engaged in significantly more territorial behaviour than males of lower social status (chi-square=43.8, $p<.001$). Significant differences existed between all status levels for males. Although there was no difference between intermediate and subordinate females, both these categories engaged in significantly less ($p<.05$) territorial behaviour than dominant females.

Table 6.12 Number of territorial acts observed for male and female rabbits of different social status.

Sampling method	Males			Females		
	Dom	Int	Sub	Dom	Int	Sub
Transect sampling	24	17	7	9	1	2
Focal sampling	68	43	14	6	3	3
Total	92	60	21	15	4	5

Dom = dominant, Int = intermediate, Sub = subordinate

Although rabbits defecate and urinate frequently within their home ranges, in order to demarcate the area (Mykytowycz 1964, 1967), these two activities were rarely seen (as mentioned in section 6.2.1). Nevertheless, the territorial function of these activities is important. The faeces of the rabbit are impregnated with odoriferous substances from the anal glands. By discharging urine and faeces within their home ranges at specific sites (dung-hills) and randomly, rabbits advertise their possession of an area to intruders. Enhanced territorial confidence also results from the presence of familiar odours (Mykytowycz and Gambale 1965, Mykytowycz 1973, 1975, Mykytowycz et al. 1976). Dung-hills or pellet heaps were most common around the entrances of well used burrows.

6.2.9 Aggressive behaviour

The aggressive category included five behaviours (viz. threat and move away, chase and chased, and fighting). As with the reproductive behaviours, these were paired activities. Overall, aggressive behaviour comprised 1.47% of transect sampling observations and 0.14% of focal sample time.

There was a decrease in the frequency of aggressive behaviour as the activity became more intense (Table 6.13). Most agonistic encounters (64%) were confined to the mildest form of aggressive behaviour, the threat and move away activities. In 31% of cases the interaction took the form of the more vigorous chase behaviour. Only in 5% of aggressive encounters did the interaction progress to the most intense of agonistic activities, fighting. Even when fighting did occur it was usually brief in duration, seldom lasting more than several seconds. Although severe fighting, sometimes leading to death, has been reported (Mykytowycz 1958, Lockley 1961, Myers and Poole 1961) it was not observed during this study. These previous studies were conducted in enclosures and prolonged aggressive encounters were often the result of experimental manipulation of established social groupings or unnaturally high population densities. Within such enclosures the rabbits' escape distances

were much reduced compared with the natural environment, and this probably contributed to the severity of the fighting.

Another noticeable feature is the higher incidence of aggressive behaviours for male rabbits. Overall, 67% of the observations (both sampling methods) of aggressive activities of marked rabbits were attributed to males (cf. 33% for females). Although this trend is evident for each of the activities within the aggressive category, the greatest difference between males and females was seen for fighting; the chase/chased interaction showed the least. When the transect sampling data for months with at least 100 observations for each sex were examined, the difference was shown to be significant (Wilcoxon signed-ranks test, $p<.05$). Overall, 2.2% of transect sampling observations on male rabbits were of behaviours in the aggressive category compared with only 1.2% for females. Other studies (e.g. Mykytowycz and Rowley 1958, Mykytowycz and Fullagar 1973) have recorded considerably higher levels of aggression, but their results were for rabbits kept in enclosures at markedly higher population densities than in this study.

Table 6.13 Number of occurrences of the behaviour groupings within the aggressive category for male (M) and female (F) rabbits.

Sampling method	Threat/move away		Chase/chased		Fighting	
	M	F	M	F	M	F
Transect sampling	66	26	32	26	6	1
Focal sampling	162	73	58	42	16	3
Total	228	99	90	68	22	4
%	70	30	57	43	85	15

Some seasonal variation was evident; higher levels of aggression in winter and spring months were associated with the consolidation and maintenance of social group territories (see section 7.2.2) and the breeding season. When breeding ceased, in the late summer months, the level of

aggression decreased with the breakdown of social boundaries. However, an increase occurred in autumn, when juveniles were dispersing and attempting to become members of establishing social groups. Young rabbits are often the target of aggressive behaviour by adult rabbits (Myers and Poole 1961), especially adult females (Southern 1948, Lockley 1960).

Most of the seasonal variation is accounted for by male rabbits. The amount of aggressive behaviour male rabbits exhibit is significantly higher in winter months and significantly less in summer months than at other times of the year (Duncan's new multiple range test, $p<.05$). The intensity of aggressive behaviour shown by male rabbits seemed to reach a peak when females were in oestrus (Southern 1948, Myers and Poole 1961). At this time the dominant male usually remained close by the female and was especially aggressive towards all rabbits, particularly other males, that ventured too close. There was no difference between any of the seasons in the amount of aggressive behaviour exhibited by female rabbits, although they were particularly aggressive if disturbed while digging.

A similar trend for the frequency of aggressive behaviours with respect to sunset time was exhibited in all seasons (Figure 6.18), although in summer the overall level of aggression was significantly less (Duncan's new multiple range test, $p<.05$) compared with other times of the year. The frequency of aggressive behaviours increased throughout the afternoon observation period reaching a peak at or slightly after sunset. This is closely related to the level of emergence of the population, with higher numbers of rabbits emerged presenting more opportunities for aggressive encounters.

Social status was an important determinant of the amount of aggressive behaviour, especially for male rabbits (Table 6.14). Dominant males exhibited significantly more aggressive behaviour than intermediate males (chi-square=6.18, $p<.02$), and intermediate males were significantly more aggressive than subordinate males (chi-square=5.93, $p<.02$). There was no difference between dominant and intermediate females, although both these

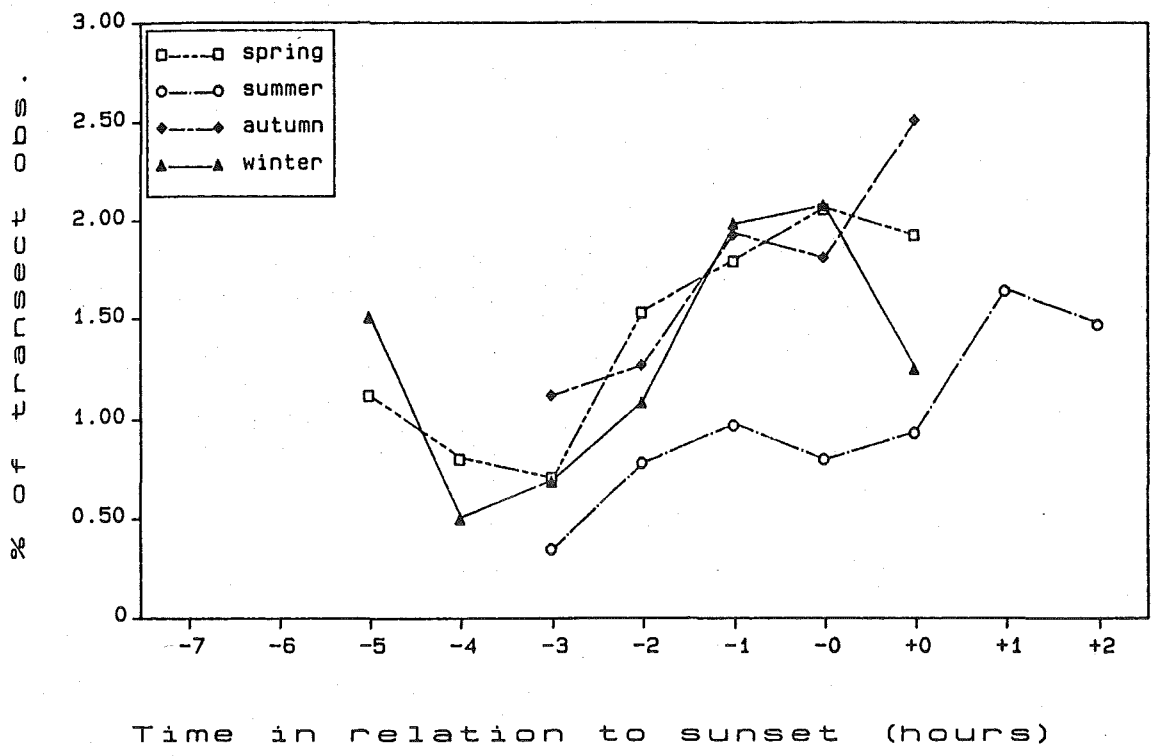


Figure 6.18 Pattern of aggressive behaviour in relation to sunset time indicated by transect sampling results pooled by season.

Table 6.14 Number of aggressive acts observed for male and female rabbits of different social status.

Sampling method	Males			Females		
	Dom	Int	Sub	Dom	Int	Sub
Transect sampling	66	55	34	41	45	17
Focal sampling	91	60	46	39	33	17
Total	157	115	80	80	78	34

Dom = dominant, Int = intermediate, S = subordinate

groups were significantly more aggressive than subordinate females (chi-square=16.51, p<.001). Similar findings have been reported by Mykytowycz and Rowley (1958), Myers (1966) and Myers et al. (1971).

Intrasexual aggression was markedly more common than intersexual aggression (Table 6.15). Intersexual aggression has been observed regularly in previous studies (Southern 1948, Mykytowycz 1958, Lockley 1961, Myers and Poole 1961). However, the intensity of the interaction appears lower than in intrasexual encounters.

Table 6.15 Frequency of inter- and intrasexual aggressive encounters noted during transect sampling observations.

Encounter type	Number of observations		%
Intersexual: M-F		78	25.5
Intrasexual: M-M	145	228	74.5
F-F	83		

M-F = male-female, M-M = male-male, F-F = female-female

On numerous occasions several activities within other behaviour categories appeared to be displayed in an aggressive context, as described for

thumping in section 6.2.6 and enurination in section 6.2.7. Another such activity was feeding: Southern (1948) and Lockley (1961) have previously noted feeding as a form of aggressive display. Aggressive feeding is characterised by violent actions where the vegetation is ripped from the ground but not ingested, and usually precedes threat or chase behaviour. Each of the activities described in the following section on displacement behaviour were observed in similar circumstances, although they were not restricted to aggressive encounters.

6.2.10 Displacement behaviour

The displacement category is composed of four behaviours (viz. scraping, paw-shake, hayraking, and challenging). Behaviours in this category were extremely rare, comprising only 0.16% of transect sampling observations and 0.11% of focal sampling time. The most frequently observed displacement behaviour was scraping, contributing 68% of all displacement activity recorded. The paw-shake and hayraking behaviours accounted for 20% and 11% of displacement activity respectively, while challenging (1%) was observed only twice over the entire duration of the study.

As with territorial and aggressive behaviour, displacement behaviour was significantly more frequent among males (chi-square=55.31, $p<.001$) although the distinction between the sexes is not as marked for the paw-shake activity compared with the other displacement behaviours (Table 6.16). The most likely explanation lies in the origin of each activity. The focal sampling data were examined to see what other behaviours were associated with the displacement activities (i.e. what preceded and followed displacement behaviour). In most cases (95%) scraping, hayraking, and challenging occurred in an agonistic context; these activities commonly accompanied territorial or aggressive behaviour sequences. However, only 21% of paw-shake observations during focal sampling were in a territorial or aggressive context. Most paw-shake behaviour (67%) was associated with grooming activities. The remaining 12% of paw-shake

Table 6.16 Frequency of behaviours within the displacement category for male (M) and female (F) rabbits.

Sampling method	Scraping M	Scraping F	Paw-shake M	Paw-shake F	Hayraking M	Hayraking F	Challenging M	Challenging F
Transect sampling	19	0	5	2	3	0	0	0
Focal sampling	44	4	9	6	6	0	1	0
Total	63	4	14	8	9	0	1	0

observations were in the context of resting or feeding behaviour.

There were so few observations of displacement behaviour each month that it was very difficult to test for seasonal patterns within this category. However, the trend was towards higher levels of displacement behaviour in autumn and winter months, as well as an overall increase as the study progressed. This last feature is most likely to be associated with the corresponding increase in population density over that time.

No trends in the incidence of displacement behaviour in relation to sunset time were evident although the small sample size may have contributed to the absence of any pattern. Male rabbits of dominant and intermediate social status exhibited a significantly higher level of displacement behaviour than subordinate males (chi-square=13.15, $p<.01$). A significant difference also existed among females, with dominant females showing more displacement activity than both intermediate and subordinate females (chi-square=7.60, $p<.05$).

The traditional view of displacement behaviour as the seemingly functionless outlet that emerges when two antagonistic drives are activated (Tinbergen 1953, Marler and Hamilton 1966, Johnsgard 1967) does not seem to fit the majority of observations here. In fact, except for the paw-shake activity, the displacement behaviours may be more appropriately classified within the aggressive category. The majority of hayraking and scraping

observations involved two rabbits simultaneously engaged in such behaviour, suggesting that these activities could be important visual signals, especially since they were frequently associated with more specifically directed aggression. Several features exhibited by the displacement category such as sex and status effects, and seasonal trends were similar to those for the territorial and aggressive categories. Marsden and Holler (1964) recorded scraping as part of the aggressive repertoire of the swamp rabbit; this activity occurred most frequently between rival males.

Only the occurrence of the paw-shake activity within an aggressive context appears to conform to the traditional description of displacement behaviours. As with most commonly quoted examples of displacement behaviour, the paw-shake activity is derived from "comfort movements" (Johnsgard 1967). In fact, most instances of paw-shake behaviour were within the context of grooming behaviour.

6.3 General Discussion

In general, activity budgets for rabbits observed in this study are similar to the results of previous studies, even though there is considerable variation in the period of observation. Most other studies (e.g. Mykytowycz 1959-61, Myers and Poole 1961, 1962, Lockley 1961, Gibb et al. 1978) have been carried out on enclosed populations, sometimes held at unnaturally high population densities. This accounts for the overall lower incidence of territorial and aggressive behaviour in this study. The levels found for most other behaviour categories are comparable to other studies.

One interesting difference noted relates to the tail-flagging activity which has previously been recorded in the reproductive category (Southern 1948, Thompson and Worden 1956). In this study it was confined to territorial encounters, most commonly intrasexual and between rabbits of different social groups. Consequently, it was placed with the other two territorial activities, chinning and patrolling. Significantly, Myers and Poole (1961) in their study

of the behaviour of wild rabbits in confined populations did not record tail-flagging in their detailed description of all activities associated with reproduction.

Although the two sampling methods used exhibited the same general trends within each of the behaviour categories, some minor differences were evident (Table 6.17). Higher levels of the least common behaviours (alert, reproductive, territorial, aggressive, and displacement) were recorded during transect sampling compared with focal animal sampling. This occurred because such activities were, by nature, more noticeable and interesting, leading to a certain amount of observer bias. Focal sampling probably gave a more reliable indication of the absolute frequency of these behaviours (Altmann 1974). However, this bias did not detract from the information obtained, for with their overall low incidence, there was a premium on gathering as much information as possible on the various activities within these categories.

Table 6.17 Percent occurrence for the 10 behaviour categories for transect and focal sampling observations, February 1981–October 1982.

Behaviour category	Percent of observations	
	Transect sampling	Focal sampling
Miscellaneous	0.12	0.14
Feeding	64.71	61.17
Grooming	4.88	4.47
Resting	20.62	32.14
Locomotory	5.93	0.97
Alert	1.03	0.06
Reproductive	0.65	0.62
Territorial	0.43	0.18
Aggressive	1.47	0.14
Displacement	0.16	0.11

Focal sampling was not without its disadvantages and biases either. The need to concentrate on observations of marked rabbits led to a high proportion of focal samples being recorded for rabbits who were in the resting position

at the beginning of the sample. This was because the identification of stationary rabbits was easier, and probably contributed most to the marked difference between transect and focal sampling results for the resting behaviour category. Some of the variation for the locomotory category is probably accounted for by the same reason. Also, much movement occurs in the context of other activities. With a 5-second limit on transect sampling observations, it was rarely possible to identify whether this was the case. In contrast, focal sampling was well suited to identifying movement in the context of other activities, with the consequence that many of these movements were properly assigned to other behaviour categories.

More important than absolute values for the behaviour categories are the relative differences that exist seasonally and between various segments of the population. Most burrow-related behaviour involved construction of breeding stops by female rabbits, and was therefore concentrated in the breeding season. Subordinate females dug more frequently as dominant females generally used established burrows in which to drop their litters.

Feeding was the predominant activity during the observation period and varied in relation to the quantity and quality of the vegetation available. Female rabbits generally spent more time feeding than males, especially during the breeding season when pregnancy and lactation increased their metabolic requirements. Similarly, after initially low levels young rabbits spent more time feeding than adults due to the higher energy requirements associated with growth.

Very little variation existed for grooming behaviour which is generally more important in the early morning activity period (Thompson and Worden 1956, Myers and Poole 1961, Gibb et al. 1978). Young rabbits did spend slightly less time than adults grooming, but no significant differences existed between males and females.

Male and female rabbits spent similar amounts of time resting, except at higher population density when males spent slightly less time resting. Young

rabbits spent more time resting in early summer but as the time they spent feeding increased, the time spent resting decreased accordingly.

Behaviours in the locomotory and alert categories were reasonably constant for adult rabbits with little variation between males and females. The significant difference between males and females for the amount of locomotory behaviour in transect sampling results is probably related to the observational bias of this method discussed above. Young rabbits spent considerably more time on activities within these two categories compared with adult rabbits.

Marked differences existed within each of the four remaining (social) behaviour categories. Social behaviour was at a peak immediately prior to, and during the breeding season. Apart from reproductive activity, social interactions were usually intrasexual and more common amongst male rabbits. Young rabbits rarely engaged in social activity, although some basic reproductive behaviours were observed in relatively young individuals.

The amount of territorial, reproductive, and aggressive behaviour exhibited was related to a rabbit's social status, both for males and females. The importance of display for the maintenance of social hierarchy positions was confirmed with a relatively low proportion of conflict situations concluding in fighting. The behaviours in the displacement category are probably better placed within other categories (e.g. scraping and hayraking were almost invariably observed as components of aggressive encounters between two rabbits).

7 SOCIAL ORGANISATION

7.1 Introduction

The social organisation of the rabbit is well documented (e.g. Mykytowycz 1958-61, Myers and Poole 1959, 1961, 1962, Lockley 1961, Mykytowycz and Gambale 1965). Studies undertaken in enclosures suggest that the social organisation of a rabbit population is likely to alter its genetic structure compared with the structure of an ideal panmitic population of similar size (Daly 1979). Social organisation can also act to reduce effective population size (Myers et al. 1971, Mykytowycz and Fullagar 1973). Although social behaviour is not the only factor regulating population size, it probably influences the effectiveness of many other factors involved in population regulation (Chitty 1967).

A variety of patterns of social organisation in rabbit populations have been described. Division of the population into separate social groups is most pronounced during the breeding season (Mykytowycz 1959, 1960, Myers and Poole 1961). Group structures can persist throughout the year, although the non-breeding period is often characterised by dispersal movements (mainly by young rabbits) and some interchange of rabbits between groups (Mykytowycz and Gambale 1965). Many mammals, especially rodents, have a particular propensity to form small breeding groups (demes) as a consequence of their social organisation (Anderson 1970, Selander 1970).

Mykytowycz (1958, 1959) and Myers and Poole (1959) found that social groups in their enclosure studies commonly consisted of 2-3 adult males and 3-4 adult females. A rigid linear hierarchy existed among the males and in effect the dominant male controlled the group. A similar hierarchy was present among females, although not as clearly defined. Dominant rabbits chased or threatened their subordinates frequently with no obvious provocation, probably aimed at emphasizing the social hierarchy within the group. In this type of group the dominant male attempts to monopolise all the adult females within

the group, and is especially attentive to females in oestrus. Unattached or satellite males were sometimes present and were quick to take advantage of the absence of the dominant male from a group. Social group territories are defended against intruders by most members of the group, including subordinate males. Subordinate females and young rabbits, however, play no significant part in defense of social group territories (Myers and Mykytowycz 1958).

Some social groups include close associations by pairs of rabbits of equal status, with the dominant male and dominant female forming a pair and so on (Lockley 1961). In those cases where female rabbits come into oestrus synchronously it is difficult for the dominant male to shield all the females from other males in the group. In an extension of this arrangement, some rabbit populations may be divided into a large number of small social groups with only one male and female per group (Parer 1977).

These previous studies suggest that group structure is dynamic and highly variable, and is probably dependent upon population density as well as a number of environmental variables which affect the dominant male's ability to maintain control over the social group's territory. It is possible that the behaviour of enclosure populations is not truly representative of the behaviour of a natural population which is likely to be more complex. In a field study of a natural rabbit population at Urana, Daly (1979) reported that most social groups in 1975 consisted of a pair of rabbits, whereas in 1976 most groups consisted of two males and two females. Only in a few of these groups did breeding pairs form; in most groups a linear social order was established among both males and females.

The effects of social organisation are not restricted to the ecology and dynamics of the population as a whole. Significant correlations exist between a female rabbit's social status and productivity, and the growth rate and subsequent social status of progeny (Mykytowycz 1959, 1960, Myers and Poole 1962). Social status is also related to juvenile and adult survival (Henderson 1979). This arises mainly because dominant females are able to monopolise the

best breeding sites within the group's territory, while subordinate females are forced to establish isolated breeding stops in areas of inferior quality (Mykytowycz and Gambale 1965, Mykytowycz and Fullagar 1973). This characteristic behaviour of dominant females resembles the tendency among dominant individuals of other species to keep to the centre (or safest place) within the group (McBride 1964).

Similar patterns of social organisation have been found for other lagomorph species, for example cottontails and swamp rabbits (Marsden and Holler 1964). These species are characterised by the formation of social groups during the breeding season, with rigid linear hierarchies amongst the males and less clearly defined hierarchies amongst the females.

Social group formation immediately prior to the breeding season is a function of mutual attraction between females (Myers 1966). The territorial conservatism of adult females is the stable basis around which dominant bucks concentrate their activities and maintain their "sphere of influence" (Southern 1940).

This chapter outlines the main features of the social organisation of the population on the Butchers Dam study area. Particular attention was given to investigating the distribution and composition of social groups over the duration of the study, the incidence of social behaviour and dominance relations outside the breeding season, and the changes which occurred following the disappearance of rabbits killed during the poison experiment.

7.2 Results and Discussion

Information on the social organisation of the population was compiled from transect, focal, and incidental observations. Observations of reproductive, territorial, aggressive, and displacement behaviour have enabled social group structures to be outlined. Collectively, these behaviour categories comprise all aspects of rabbit social behaviour. In addition, association patterns have been calculated from transect data. Odoriferous

gland weights from autopsy of marked rabbits killed during the poison experiment have provided additional evidence of the social status of individuals.

Although a considerable proportion of the population remained unmarked throughout the study (see section 9.2), there was sufficient information available to ascertain the structure of most groups on the study area, especially those which occupied group territories within the fence line. Except where unidentified rabbits were important (dominant) members of a social group, this category has been excluded from the results. Without individual identification social group attachment could never be established with complete reliability.

7.2.1 Maintenance of social structure

The mechanism by which social groups are established and maintained is the dominance hierarchy. Dominance hierarchies result from agonistic encounters between rabbits of the same sex (see section 7.2.3).

Dominance matrices were constructed to help elucidate social group structures. These include only aggressive interactions where there is a winner and a loser, i.e. threats or chases. Such a matrix for male rabbits in one social group during the period April-November 1981 is given below:

	Loser					
Winner	M16	M37	M40	M11	Wins	Losses
M16	-	4	4	7	15	0
M37		-	2	4	6	4
M40			-	0	0	6
M11				-	0	11

The linear hierarchy in this group was very clear. M16's dominant position was never challenged by the other males. There were very few reversals in status. On the rare occasions that dominant males were the losers in aggressive encounters, they were usually outside their normal ranges. The relationship

between territorial confidence and a rabbit's familiarity with its surroundings is well known (Mykytowycz 1959, Lockley 1961, Mykytowycz and Hesterman 1970).

With the exception of reproductive activity, considerably less social behaviour was observed amongst female rabbits compared with males. This is illustrated by the low number of aggressive interactions in the win-loss matrix for female rabbits of the same social group over the same period:

	Loser						
Winner	F02	F51	F05	F13	F14	Wins	Losses
F02	-	3	2	0	0	5	0
F51		-	0	0	0	0	3
F05			-	0	0	0	2
F13				-	0	0	0
F14					-	0	0

Despite the relatively sparse data for female rabbits (5 aggressive interactions, cf. 21 for male rabbits), linear hierarchies were confirmed amongst females in all social groups. Female rabbits exhibited the same range of intensity of aggressive behaviour as males. In fact, some of the most vigorous chases and fights occurred when a female was disturbed while burrowing.

Dominance hierarchies were invariably linear although, in several groups, rabbits of equivalent status were present. This was more common amongst females and generally involved rabbits less than 1 year old. Dominant rabbits engaged in aggressive encounters more frequently than rabbits of intermediate or subordinate status, as previously reported (Myers 1966, Myers et al. 1971).

Once the dominance hierarchy is established, intense aggression (e.g. vigorous chases, fighting) is generally avoided (Lockley 1961). Much of the maintenance of social group structure was achieved with the less aggressive interaction of supplanting. This occurred when a dominant individual approached a subordinate and, without any threat behaviour, the subordinate

rabbit moved away. This type of interaction was not identified until late in the study when a knowledge of the social structure of the population allowed a better understanding of some sequences of behaviour. Consequently, supplanting was never included as a behaviour within the aggressive category. However, during winter and spring 1982, reinforcement of social rank by supplanting appeared to be more common than reinforcement by other more aggressive activities (i.e. threats and chases).

The concept of individual distance is relevant here; the rabbit conforms to Brown's (1975) description of a "distance species" where body contact normally occurs only in sexual or agonistic contexts. Rabbits maintain an individual distance between themselves and others. For male rabbits the individual distance was about 1-1.5 m, whereas females often fed peacefully less than 0.5 m from each other. Similarly, male-female distances were smaller than male-male distances.

As previously established (see sections 6.2.7-6.2.10), the degree of sociality of an individual was strongly correlated with its social status. Amongst male rabbits the distinction between all three social status levels is considerable; dominant males were responsible for nearly 50% of all social interactions observed, with intermediate and subordinate males accounting for approximately 30% and 20% respectively (Table 7.1). Variation between female rabbits of different social status was not as marked. Dominant and intermediate females exhibited similar levels of social behaviour, and accounted for twice as much social activity as subordinate females.

7.2.2 Seasonal incidence of social behaviour

The level of social behaviour observed in the population fluctuated throughout the year (Figure 7.1) with more social behaviour in winter and spring months, when breeding was occurring in the population, compared with summer and autumn months. The pattern from reproductive activities was different from the other activities that are included within social behaviour.

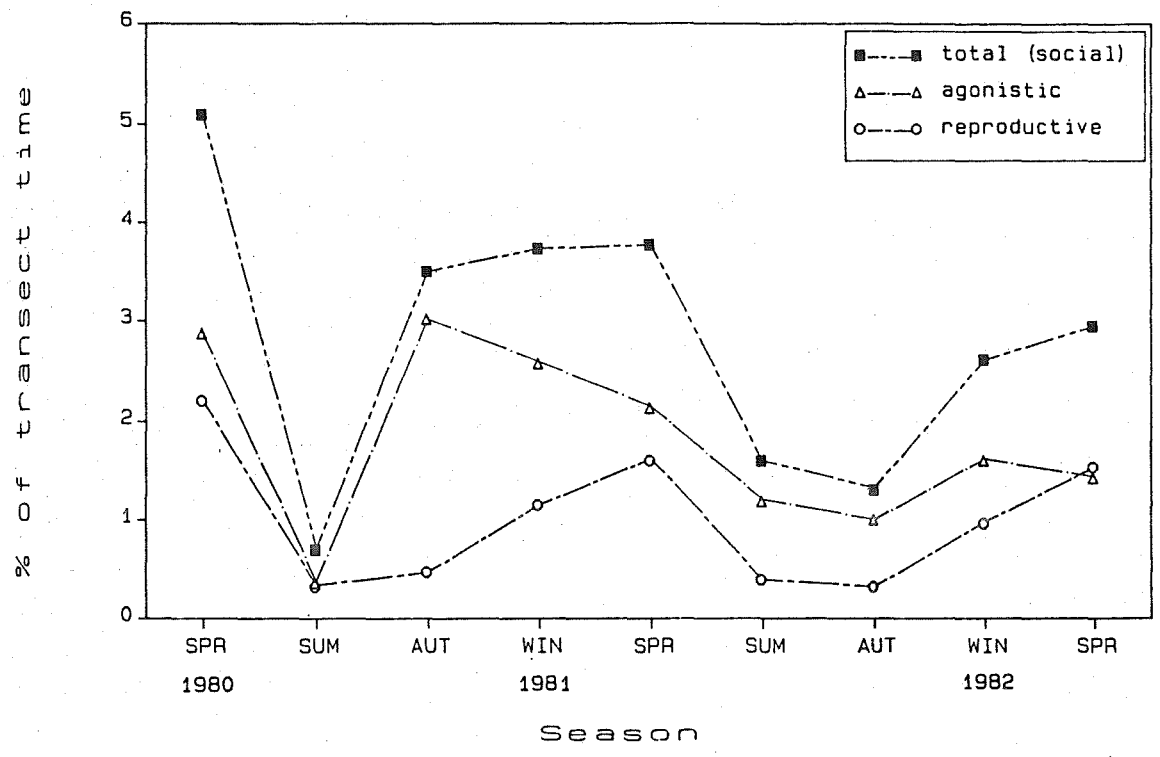


Figure 7.1 Frequency of reproductive and agonistic (territorial, aggressive, and displacement) behaviour indicated by transect sampling results pooled by season.

Table 7.1 Distribution of all social behaviour observations in relation to social status for male and female rabbits.

Social behaviour category	Males			Females		
	Dom	Int	Sub	Dom	Int	Sub
Reproductive	97	51	27	45	58	25
Territorial	92	60	21	15	4	5
Aggressive	157	115	80	80	78	34
Displacement	42	41	16	10	3	2
Total	388	267	144	150	143	66
%	48.6	33.4	18.0	41.8	39.8	18.4

Dom = dominant, Int = intermediate, Sub = subordinate

Whereas reproductive behaviour was more clearly seasonal, the incidence of other social behaviour was somewhat irregular. Aggressive behaviour comprised the majority (64%) of these other activities and accounts for the seasonal trend (Mykytowycz and Fullagar 1973, Mykytowycz and Hesterman 1975).

The high level of non-reproductive social behaviour in autumn 1981 does not seem to fit the pattern of the rest of the data. It is possible that population changes were responsible for this difference. Several studies (e.g. Chitty 1960, 1967, Christian and Davis 1964, Krebs et al. 1973) have shown that population substructure (i.e. social organisation) and demographic processes can affect the behaviour of individuals. In fact, social organisation effects were postulated as possible regulating factors for population density (Wynne-Edwards 1962, 1965, Chitty 1967). Over the preceding months the population on the study area almost doubled (see Figure 9.1). Excluding the effects of the poison experiment, this was the most marked change in density over the duration of the study. The high level of aggression in autumn 1981 may have been a reaction by resident adult rabbits who were facing increasing pressure by dispersing juveniles and subadults to associate with existing social groups during this period.

The seasonal distribution of intra- and intergroup aggression was distinctive (Table 7.2). Whereas intragroup aggression functions to maintain social hierarchies within the group, intergroup aggression acts to preserve the spatial separation of groups. This is confirmed by the high proportion (70%) of intrasexual encounters within intragroup aggression. Intragroup aggression is greatest during late autumn and early winter, the period of social group formation and consolidation of social status positions. Intergroup aggression reaches a peak during winter and spring, when breeding within the population is associated with more conservative movement patterns and rigid social group territories. Despite the wider movement of rabbits during summer and autumn months, aggression between members of different social groups during this period is at markedly lower levels.

Table 7.2 Seasonal distribution of intra- and intergroup aggressive encounters from all observations.

Season	Intragroup n	Intragroup %	Intergroup n	Intergroup %
Summer	28	15.1	20	14.9
Autumn	74	39.8	18	13.4
Winter	48	25.8	46	34.3
Spring	36	19.3	50	37.4
Total	186		134	

n = number of aggressive encounters

Almost 60% of aggressive encounters (threats, chases, and fights) occur between members of different social groups. The lower proportion of encounters between members of the same group probably reflects the relative stability of rabbit social groups and the role that the passive interaction, supplanting, plays in the maintenance of order within the group.

7.2.3 Inter- and intrasexual aggression

More than 500 aggressive interactions involving at least one marked rabbit were recorded (Table 7.3). Where both rabbits were identified, the majority of interactions (75%, 228/306) involved two rabbits of the same sex. Aggression between male and female rabbits was less frequent (25%) and usually occurred during winter and spring. Neither sex appeared to predominate, males winning 54% of encounters and females 46%.

Table 7.3 Aggressive interactions recorded for marked rabbits.

	Participant B			
Participant A	Unidentified	Male	Female	Total
Male	162	145	35	342
Female	70	43	83	196

Only 27% of intersexual aggressive encounters were between members of different groups. This suggests a greater tolerance towards rabbits of the opposite sex of different social groups, compared with rabbits of the same sex. This helps to explain why satellite males are sometimes successful in mating with females in the absence of the dominant male.

Male rabbits accounted for 64% of all intrasexual aggressive encounters. The lower frequency of aggression among females was probably a result of two factors: female rabbits exhibited a greater tolerance towards other females, as the individual distance evidence suggests, and females never competed for the attention of male rabbits.

7.2.4 Odoriferous gland weight evidence

The size and secretory activity of certain odoriferous glands in the rabbit are correlated with age, sex, social status, and reproductive condition and are hormonally controlled (Mykytowycz 1965, 1966a, 1966b, Mykytowycz and

Dudzinski 1966). The territorial role of the submandibular glands and the anal glands is well established (Mykytowycz 1965, 1966a, Mykytowycz et al. 1976). The secretions from the inguinal glands are not involved in any specific marking activities. Instead, they are considered to function in sexual attraction and individual recognition (Mykytowycz 1966b, Mykytowycz et al. 1976). These relationships were used to confirm social status rank for marked rabbits killed during the poison experiment. In addition to these glands, the submandibulary lymph nodes were also removed from marked rabbits during autopsy.

The weights for these glands are listed in Table 7.4. The difference between the weights of the submandibulary, anal, and inguinal glands for male rabbits of different social status is considerable. There was only one example of overlap between the categories; M47's submandibular gland weight was greater than that for two dominant rabbits, M37 and M76. However, the weights of the anal and inguinal glands confirm the intermediate social status of M47.

Although Mykytowycz and Dudzinski (1966) found a significant relationship between social status and the weight of the anal and inguinal glands for female rabbits, the distinction for the females listed in Table 7.4 is not clear. Poor correlations exist for all the odoriferous glands. F61 had only recently attained dominant status whereas F52 had originally been dominant before being displaced by F33 several months earlier (see section 7.2.5). However, even when these changes are taken into account, discrepancies still exist between the actual and expected rank order of gland weights.

The marked sexual dimorphism previously recorded for odoriferous gland weights (Mykytowycz 1966a, 1966b, Mykytowycz and Dudzinski 1966) was evident. Mean weights were not calculated because of the very small sample sizes involved. The difference between male and female rabbits is associated with the greater degree of territoriality among males. Submandibular lymph node weights did not exhibit the same relationship with social status as the odoriferous glands, nor was any sexual dimorphism evident.

Table 7.4 Gland weights for marked rabbits killed during the poison experiment.

Social status	Rabbit	Gland weight (mg) Submand.	Anal	Inguinal	Lymph node wt. (mg)
Dominant	M23	1056	1321	413	1100
	M37	874	2497	539	836
	M71	1326	1862	381	866
	M76	931	1426	347	851
	F42	491	461	-	921
	F61	708	374	116	930
Intermediate	M46	-	1271	204	-
	M47	1052	1102	269	1122
	M78	737	1167	341	1027
	F52	362	641	108	647
	F69	490	671	151	621
Subordinate	M64	883	887	-	831
	F24	740	460	128	697
	F66	617	228	37	815
	F177	-	441	101	-

7.2.5 Description of social organisation by season

Most previous assessments of social organisation in rabbit populations have been subjective. Recently, Fullagar (1981) examined associations between individuals as a means of interpreting other observations on social behaviour. The technique used involves the analysis of symmetrical association matrices (cf. similarity matrices in numerical taxonomy). These matrices contain information on the degree to which any two rabbits are found together. Two rabbits were assumed to be associating if they were observed within the same grid square during a transect sample.

Association data for each pair of marked rabbits were normalised by calculating Jaccard coefficients of association (Sokal and Sneath 1963) using the formula:

$$c_J = \frac{2n}{(2n+u)}$$

where c_J = the Jaccard coefficient of association,

n = the number of times two rabbits are seen together, and

u = the sum of the number of times each rabbit is seen with different rabbits (i.e. not the other member of the pair).

Using this formula, coefficients of association range from 0 (never seen together) to 1 (always seen together). The association matrix for all marked rabbits present during September and October 1982 is given below:

	F05	F23	F33	F36	F49	F84	F87	M26	M35	M41	M51	M56	M59	M67	M68	M79
F05																
F23	-															
F33	-	.12														
F36	-	-	-													
F49	.23	-	.08	.08												
F84	-	-	-	.24	.14											
F87	.10	-	-	.42	.14	.46										
M26	.10	.13	.23	-	.09	-	-									
M35	-	.72	-	-	-	-	-	-								
M41	-	-	.39	-	-	-	-	.07	.06							
M51	-	-	-	-	-	-	-	-	-	-						
M56	.19	.05	.26	-	.34	-	-	.11	-	.16	-					
M59	-	-	-	-	-	-	-	-	.19	-	.25	-				
M67	-	-	-	-	-	.18	-	-	-	-	-	-	-			
M68	-	-	-	-	-	-	-	-	-	-	.75	-	.25	-		
M79	-	-	.26	-	-	-	-	-	.08	.09	-	-	-	-	-	

A principal coordinate analysis (PCO) (Gower 1966, 1967) was used on the association matrices, which were constructed for each season. PCO analyses result in simplified representations of the association data in a reduced number of dimensions, with inter-individual association or 'distance' preserved in the 'best possible' way. Values for the first three latent vectors were plotted to give 3-dimensional representations of the rabbits' relatedness in hyperspace (Figure 7.2a). As an adjunct to the PCO analysis, a minimum spanning tree (MST) (Gower and Ross 1969) was calculated for each set of association data (Figure 7.2b). A minimum spanning tree is a network relating every individual to another so that the network of links has minimum

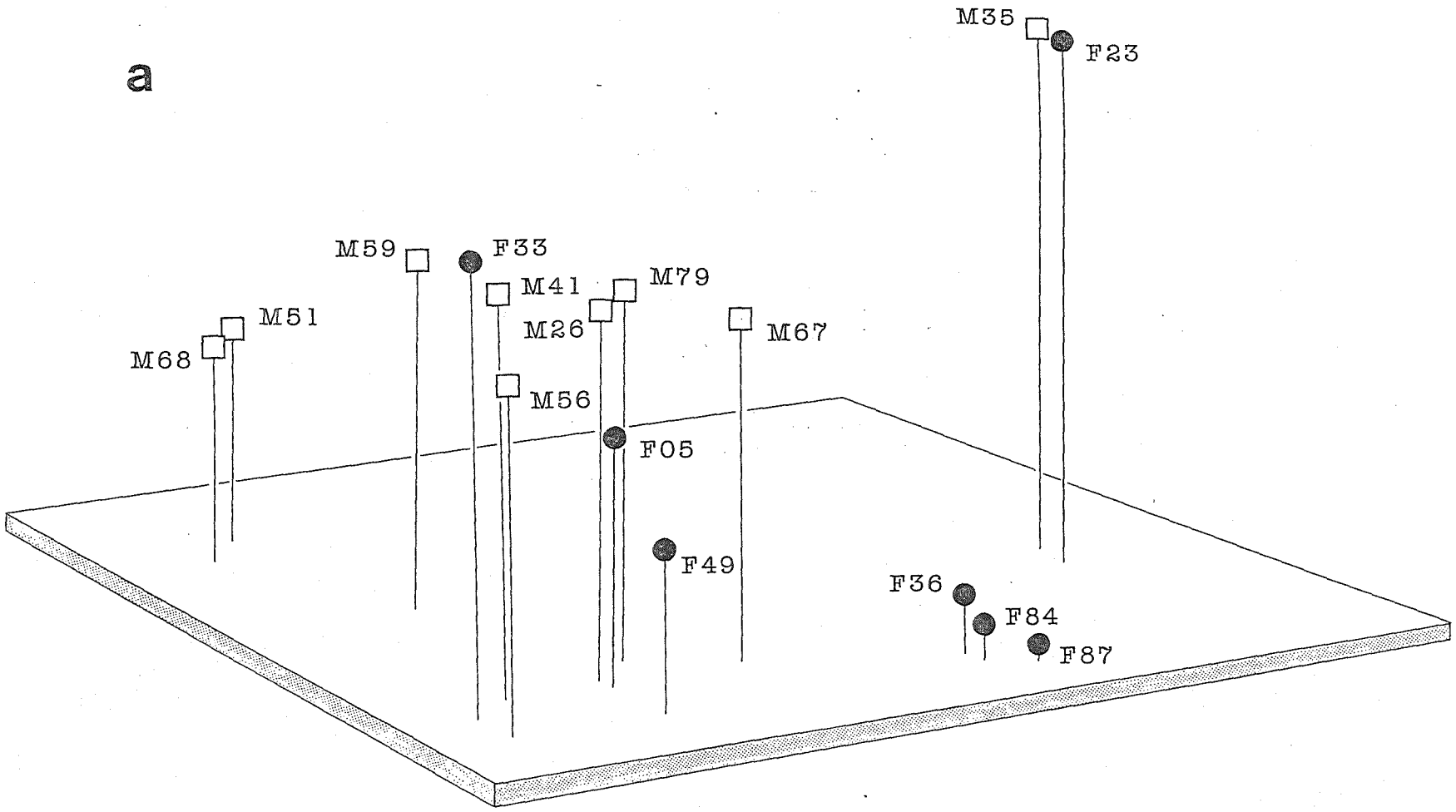
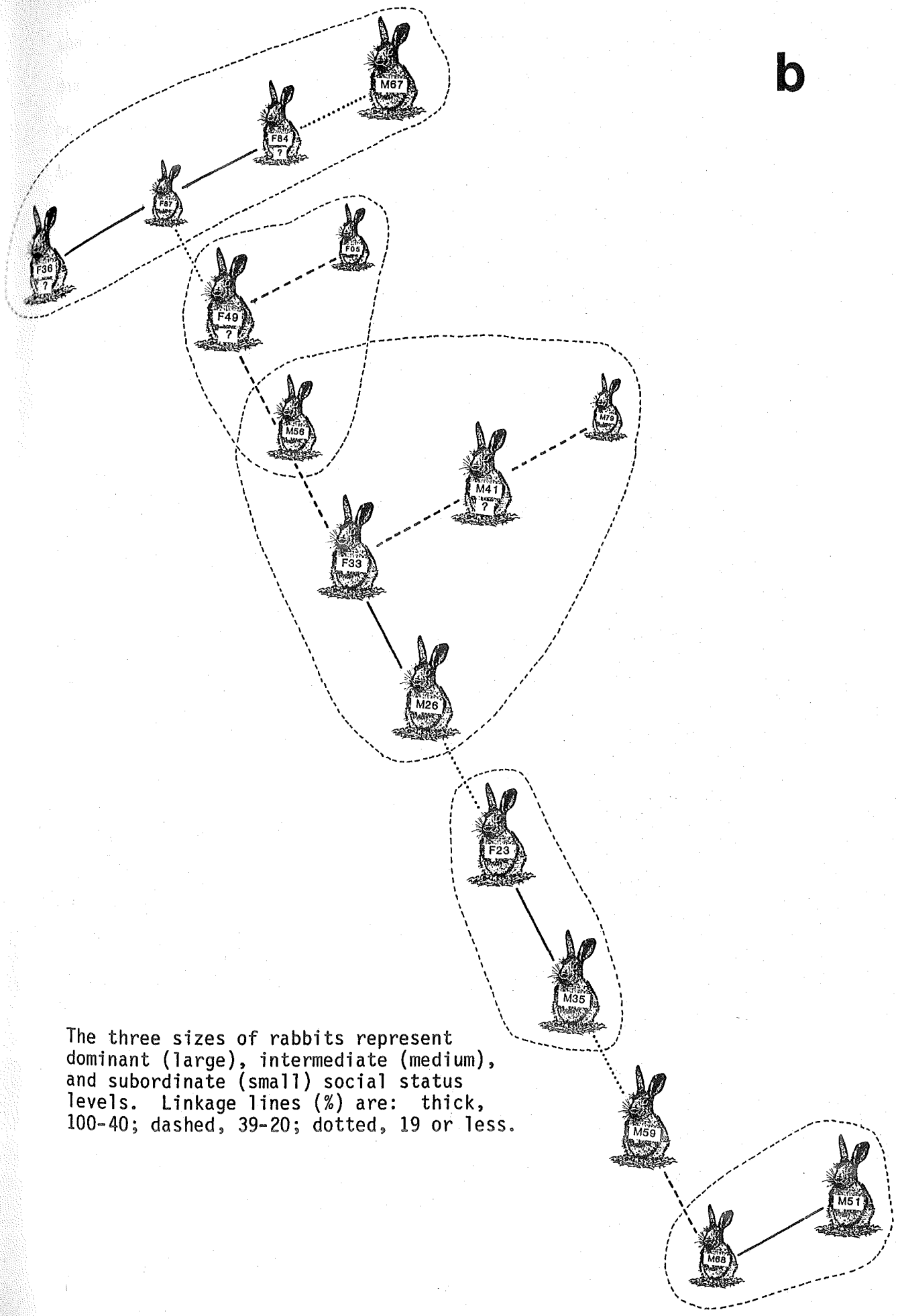


Figure 7.2 (a) Three-dimensional representation of principal coordinate analysis results and (b) a minimum spanning tree for September–October 1982 association data.



The three sizes of rabbits represent dominant (large), intermediate (medium), and subordinate (small) social status levels. Linkage lines (%) are: thick, 100-40; dashed, 39-20; dotted, 19 or less.

total length and there are no closed loops (cf. single linkage cluster analysis). Because the PCO analysis provides an approximation in a few dimensions to configurations in many dimensions, some distortion is invariably present. In this situation the MST is a useful ancillary technique aiding in the detection of any such distortion (Fullagar 1981).

Plots of PCO results and MST diagrams have been used in association with behaviour observations, win-loss matrices, and movement patterns to describe social group structures. Despite the low proportion of variance explained by the PCO analyses (Table 7.6), the patterns established from the other data were often confirmed by the PCO and MST results. However, the PCO results could never be used in isolation to establish social group membership. The low variance values are caused mainly by a large number of empty cells in the association matrices, rather than any shortage of association data (K Malafant CSIRO pers. comm.).

Table 7.6 Number of associations, percent of empty cells in the association matrices, and variance explained by the first three latent roots from the PCO analyses.

Season	Number of observations	Percent of empty cells	Percent variance
Summer 1980/81	179	76.3	21.7
Autumn 1981	119	64.1	22.0
Winter 1981	182	71.1	28.0
Spring 1981	151	71.9	23.0
Summer 1981/82	216	80.5	18.9
Autumn 1982	204	67.0	18.9
Winter 1982	424	63.8	19.6
Spring 1982	100	73.3	37.8

The best result was for spring 1982; although there were only 100 association observations, the first three latent vectors accounted for nearly 40% of the variance. The proportion of empty cells in the association matrix is similar to the other seasons but the lower number of rabbits present in

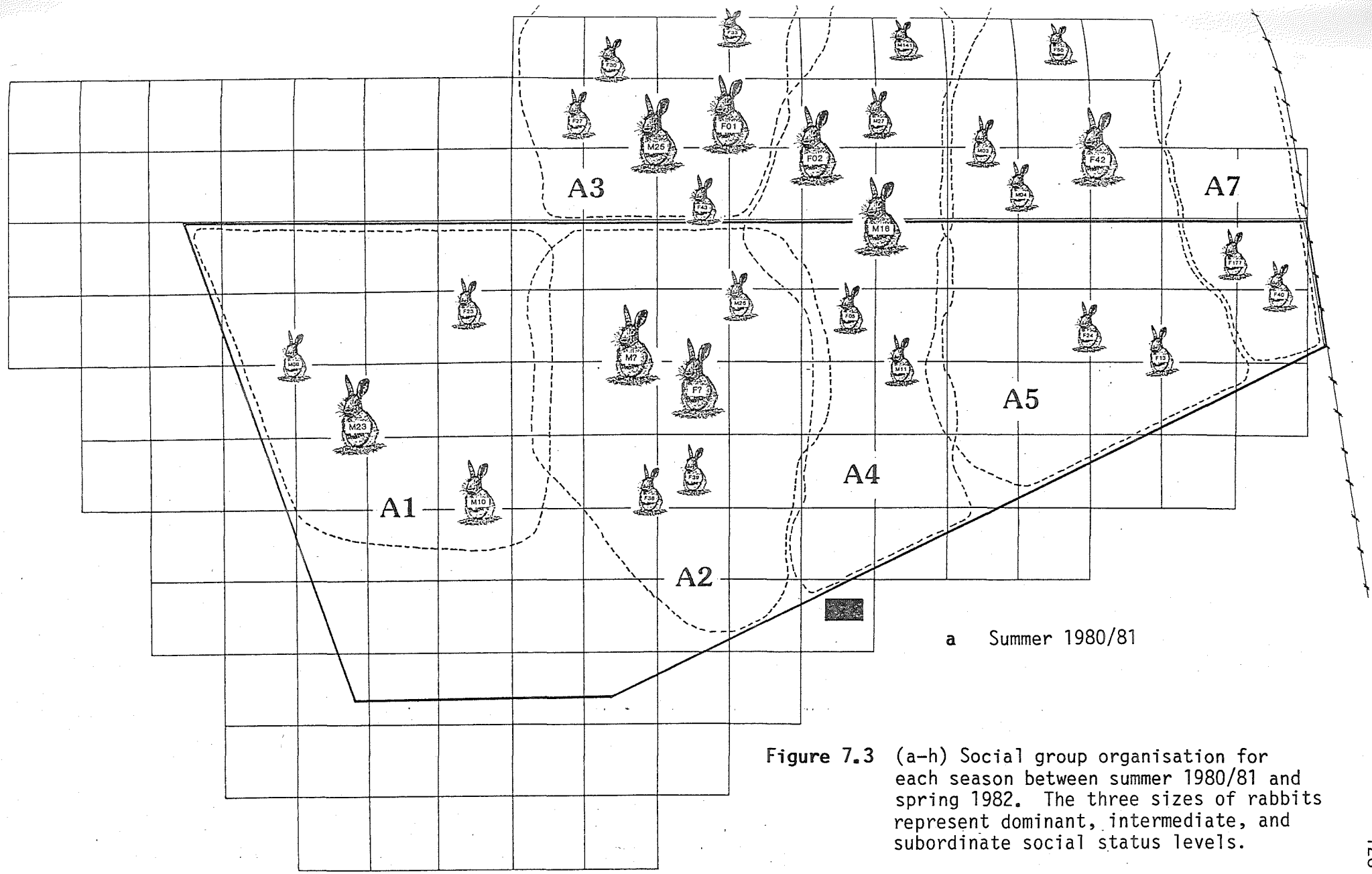
spring conferred greater weight on the Jaccard coefficients of association.

The PCO technique is best suited to analyses of small groups of rabbits, where an individual has a chance of associating with every other individual. Fullagar (1981) had only 13 rabbits in the population he described using the PCO method. In this study the size of the observed area, the number of rabbits present, and the prevailing movement patterns severely restricted the number of possible associations for each rabbit.

Brief details of the social group structures within the population for the duration of the study are described below. This information, illustrated in Figures 7.3a-h, is dealt with by season for convenience only. Some of the most noticeable changes in social structures occurred within rather than between seasons. The terminology used in the description of social group structures in this section may be confusing. Although the term "social group territory" (Mykytowycz 1959-61, Myers and Poole 1959, 1961) has been adhered to, the actual situation was not as rigid as the term implies. Boundaries between social groups were more strongly defended during winter and spring than at other times of the year (see section 7.2.2). In addition, on numerous occasions the absence of members of one social group appeared to precipitate extensions of normal activity ranges by some individuals from adjacent social groups. Therefore, although the social group territories illustrated for each season give a fair representation of the social arrangement of the population for that period, they should not be regarded as rigid or totally exclusive boundaries.

Summer 1980/81

Although the proportion of the population marked at this stage of the study was not large, a number of social groups could be identified (Figure 7.3a). Group A1 included M23(D=dominant), F23(S=subordinate), M10(I=intermediate), and M08(S). These rabbits, especially M23 who was dominant and F23, ranged over most of the left side of the area inside the



a Summer 1980/81

Figure 7.3 (a-h) Social group organisation for each season between summer 1980/81 and spring 1982. The three sizes of rabbits represent dominant, intermediate, and subordinate social status levels.

fence line. M10 was a juvenile, born about August/September, and initially moved over a smaller area than M23 and F23. However, towards the end of summer M10 appeared to be attracted to the lower parts of the A2 group territory by the presence of two young females, F38 and F39. As a juvenile, M10 was tolerated by M23 more than the subordinate adult M08, who usually maintained a safe distance from M23.

The two dominant rabbits in A2 were unidentified. This pair had resting locations within the gully situated near the centre of the area and never ventured outside the fence line. There were no other adult rabbits in this group. M26 was a young rabbit born early in the breeding season while F38 and F39 were progeny from a later litter.

Group A3 was centred on M25(D), F01(D), and several young rabbits including F27 and F30 (early litter) and F43 (later litter). The dominant pair were rarely seen apart in the early part of this season. However, towards the end of summer M25 spent more time close to the young females F27, F30, and F43.

Group A4 included M16(D) and F02(D), as well as F05, M11, M27, and M141, all young of the year. This group ranged over a large but mostly poor quality area directly in front of the observation hut. Group A5 was centred on F42(D) and included F13(S) as well as young of the year, M04, F24, and F50 (earlier litters) and M03 (later litter). This group occupied a territory adjacent to A4 but did not venture inside the fence line as frequently. Finally, several rabbits including F177(S) and F40 (young) occupied a small range on the southern edge of the study area. However, this was only part of their group territory and observations on these rabbits were few.

The summer period was characterised by the presence of numerous young. Earlier in the season territorial boundaries were strongly defended, especially in A2 and A3. By February many rabbits had begun to range further and less aggression was shown by dominant individuals to these intruders, who were often juveniles.

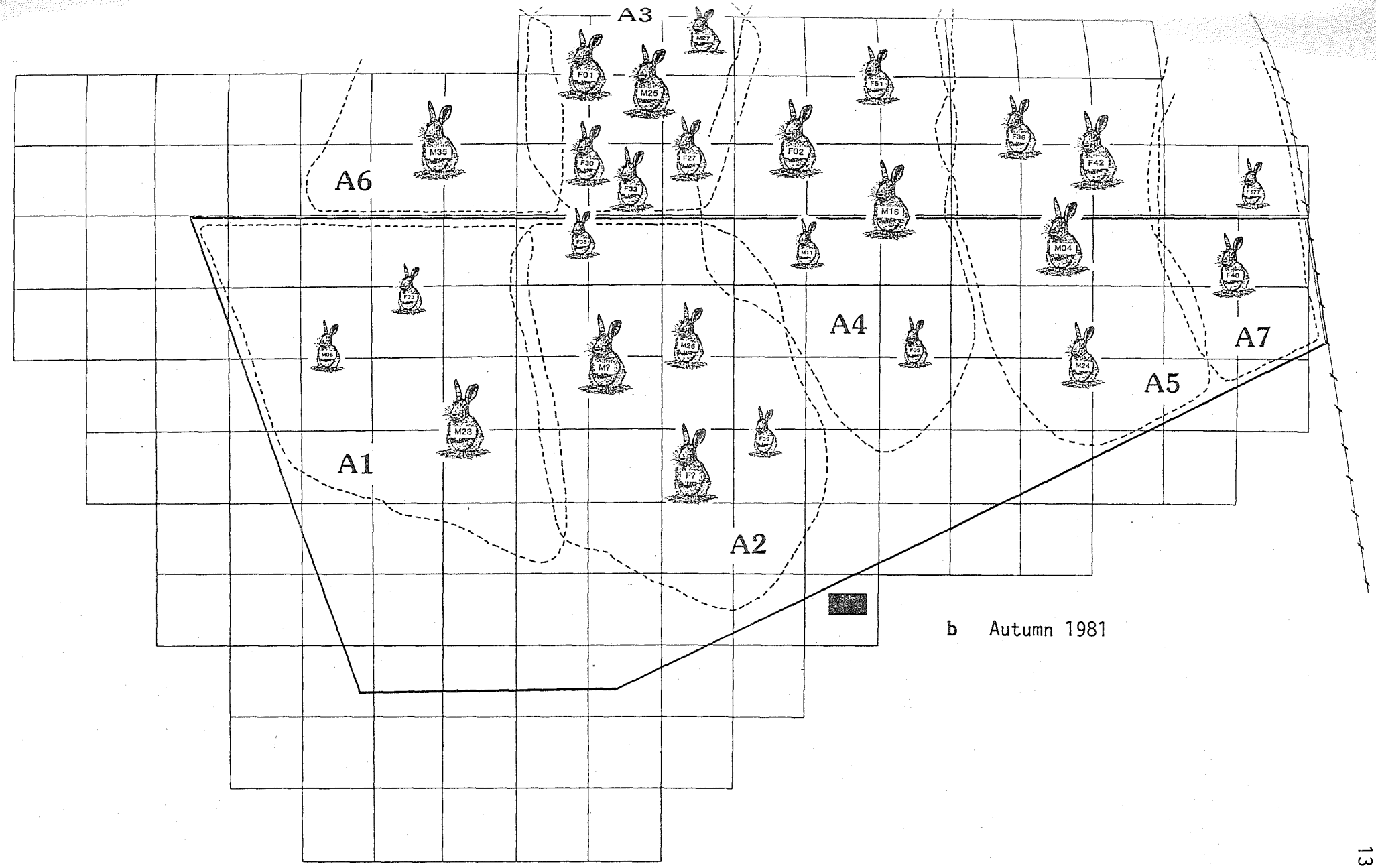
Autumn 1981

Rabbits continued to range further in this season, generally with reduced aggression between members of different social groups (Figure 7.3b). Towards the end of autumn, however, much of this movement ceased with an increase in the level of aggression between members of adjacent groups and the start of reproductive behaviour within the groups.

M23(D) continued to dominate the A1 social group although often concentrating his activities close to the A2 group territory. This led to considerable territorial and aggressive behaviour between M23 and both the unmarked dominant male and M26(I) from A2. When the unmarked male disappeared between April and May, M23 immediately moved in and took over the dominant position in the A2 territory. Simultaneously, M26(I) moved away from A2 and associated with rabbits from A3 and A4, while F38 shifted to A3 permanently. The A2 territory was better quality habitat, in terms of food supply and permanent resting locations, and this helps to explain M23's attraction to this area.

Although M25 was still dominant in A3, there was considerable movement of rabbits between this group and A4. Rabbits frequently grazed within the other group's territory. During one transect sample nine rabbits were seen grazing in one grid square (15 x 15 m) without any aggression. The dominant male from A4, M16, was noticeably absent and usually ventured into the A3 territory only when M25 was absent. Following the disappearance of F01(D) in April, F27 became increasingly aggressive towards the two other oldest females in this group, F30(I) and F33(I).

M16(D) still controlled the A4 group and towards the end of autumn was frequently seen exerting his authority. On occasions he appeared to seek out other males in the A4 group, especially M11(S), to threaten or chase them. By late autumn M16 was associating regularly with F02(D) while M11(S) was often seen near F05(S).



b Autumn 1981

Rabbits in group A5 moved less than individuals in other social groups. F42 maintained her dominant position and was often observed in aggressive encounters with males in the group. There did not appear to be a dominant male in the A5 group during this period. Only limited evidence of group A6 centred on M35(D) was available, while rabbits belonging to group A7 continued to occupy only a small part of the observed area.

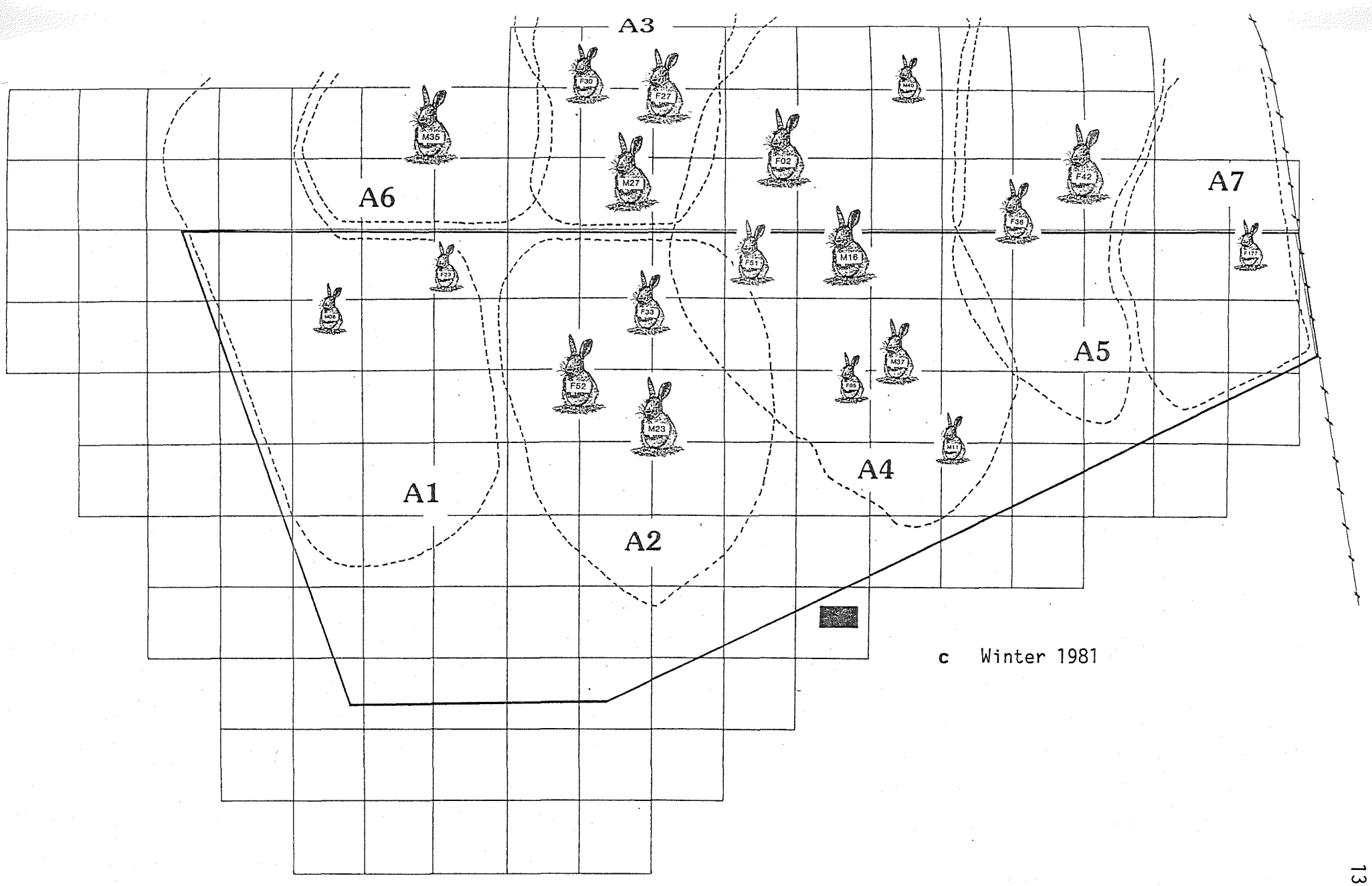
Winter 1981

This season was characterised by continued high levels of aggression and an increase in reproductive behaviour as social group structures stabilised (Figure 7.3c). Some movements occurred early in winter but these were mostly limited to permanent changes between groups rather than the previous wide ranging grazing movements.

M23(D) and F52(D) were the dominant pair in A2 and in late winter F33(I) moved from A3 to A2 possibly because of increased aggression by F27(D) and F30(I). F52 was the previously unmarked dominant female in the A2 group. F23(S) sometimes ventured close to this group, although she was also seen in the A1 and A6 territories. M23 was highly territorial and directed considerable aggression towards rabbits of group A4 who often used a smeuse trap in the top right side of the A2 group territory to move inside the fenced area.

M25(D) disappeared in June and this lead to M27 becoming the dominant male in A3. M27 usually associated with F27(D) and F30(I). There were numerous border disputes at this time between both males and females in group A3 and rabbits in the A4 group, especially M37(I).

F51(I) began to challenge F02's dominant position in A4 and was often seen associating with M16(D). M37(I) was usually seen near F05(S) although when M16 was absent M37 would consort with F51. Although M11(S) and M40(S) often defended the A4 group territory from intruders and displayed territorial behaviour, they were not tolerated close to the females and were often the



c Winter 1981

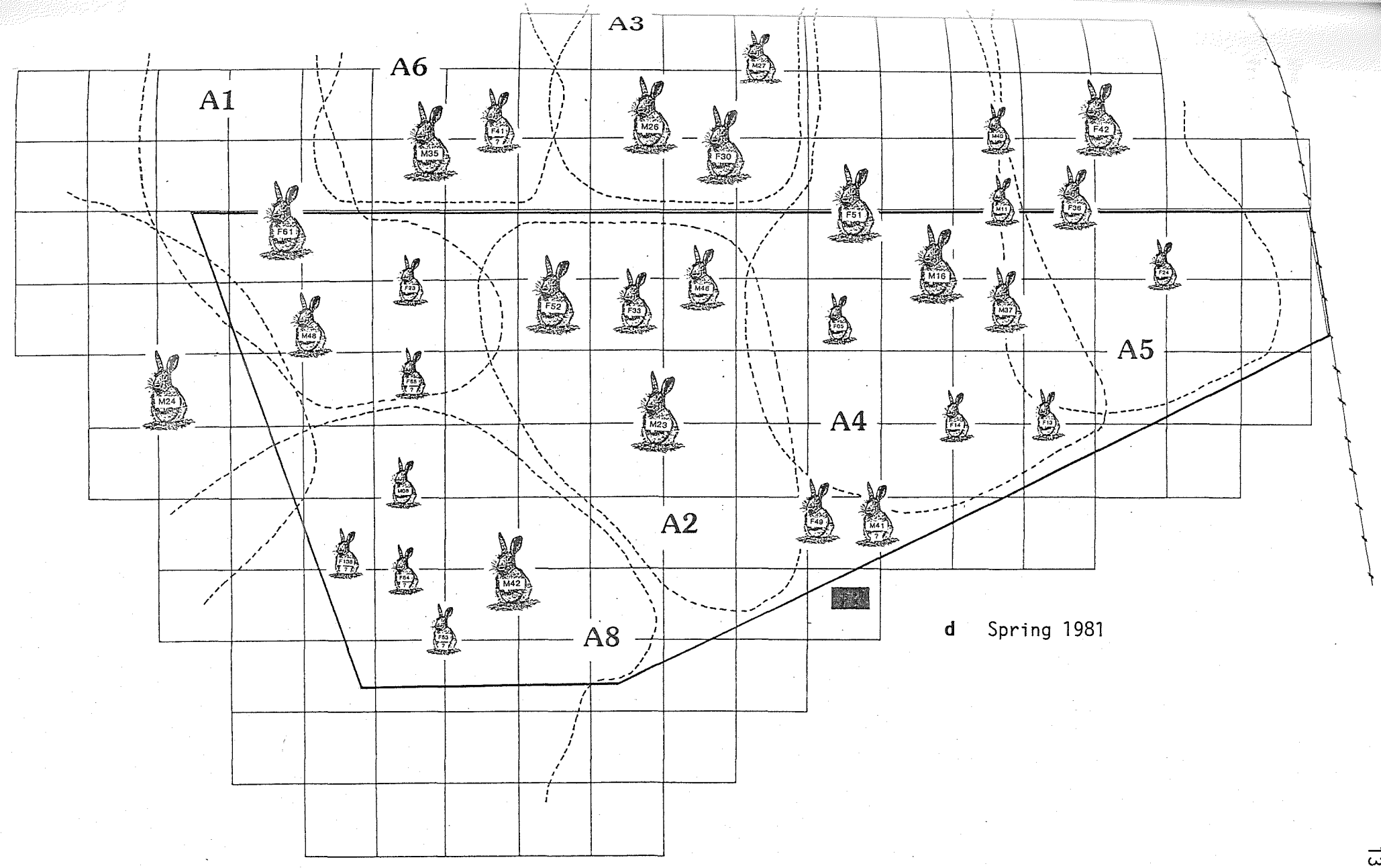
target of aggression from M16 and M37. F49 was a satellite rabbit and was sometimes seen in the border area between the A2 and A4 group territories although rabbits from both groups usually chased F49 if she got too close. F49 was not the only satellite during this period. Although basic group structures were stable a number of other satellites, mostly males, were observed ranging over much of the area. They generally kept a safe distance from other rabbits, especially dominant males.

The stability of the A5 group, based on F42(D) and F36(I), continued although very few rabbits used this area and interactions were rare. Group A7 remained mostly out of view. Although F177 was a subordinate in A7 she was observed defending the group territory from intrusions by A4 and A5 rabbits. More rabbits were starting to use the A1 area, with M08 still subordinate and generally maintaining a safe distance from other rabbits.

Spring 1981

By spring considerably more rabbits were observed on the northern side of the area and many of these were marked (Figure 7.3d). The response to the increased numbers was a split into two groups, the original A1 and a new group A8. Group A8 included M42(D), M08(S), and three females, F138, F53, and F54, whose status was uncertain at this stage. Group A1 consisted of M48(I), F61(D), F23(S), and F55. M42 spent some time in A1 and may have also been dominant over this group. F23 and F55 often ventured into the A8 range where they were tolerated but towards the end of spring both these rabbits spent more time in A1.

Strong defense of the A2 group territory by M23(D) continued. M23 associated and mated with F52(D) during the early part of spring but F33(I) began to displace F52 as the dominant female in A2 towards the end of this season. F33 became increasingly aggressive towards other females, especially the satellite F49 whenever she ventured into the A2 territory. M41 was also a satellite who regularly used the border area where groups A2 and A4 met.



d Spring 1981

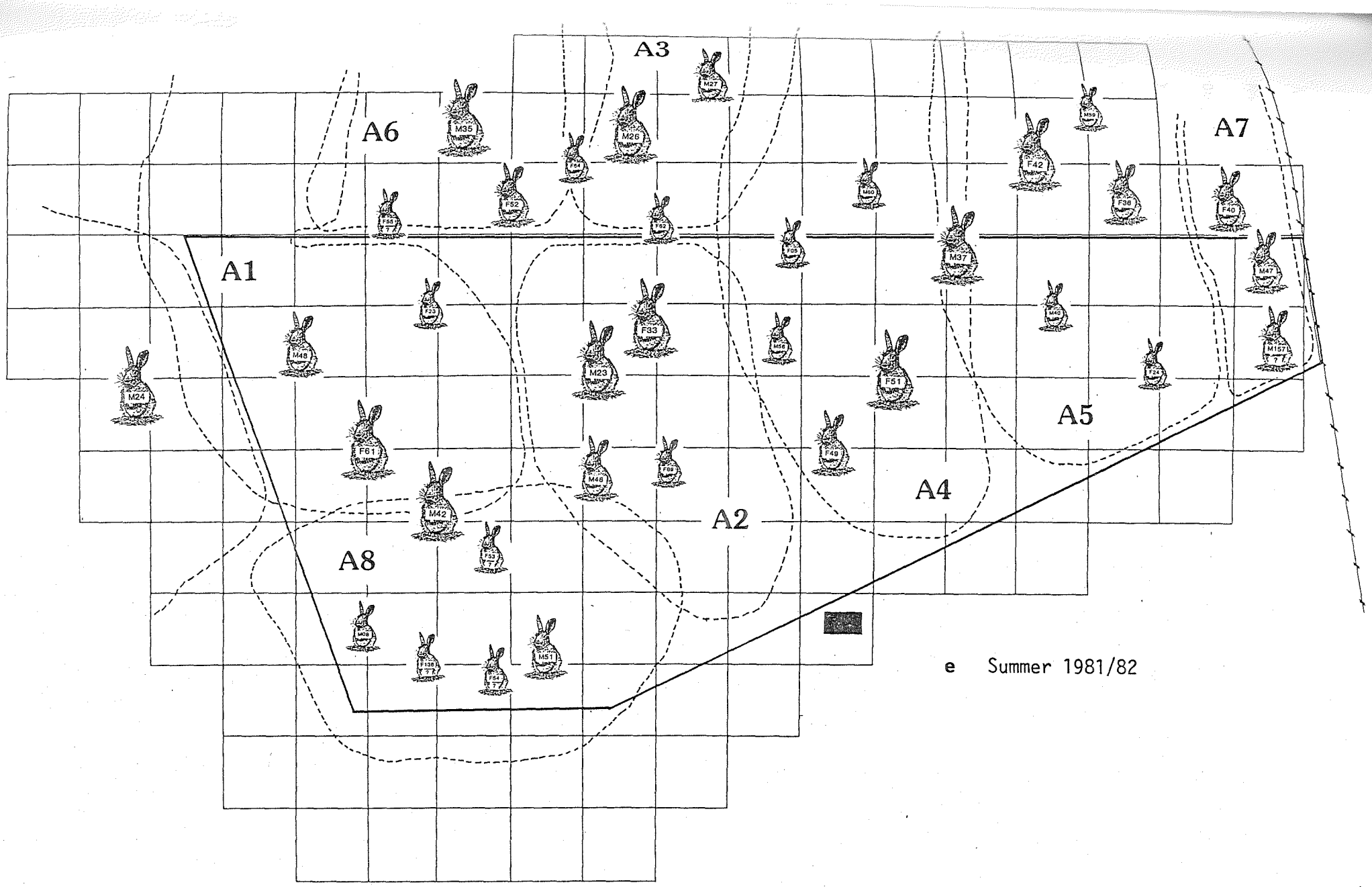
Whereas M23's dominance was never challenged in the A2 territory, he was frequently evicted from the edge of the A4 territory by a number of rabbits.

By spring F27 had disappeared from the A3 group and F30 was now the dominant female. M26 moved into A3 and took over as the dominant male displacing M27 from this position with a minimum of disturbance. Aggression between these two males was rare. M35(D) and F41 were the only marked rabbits in the A6 group which included several unmarked individuals and occupied a very small area adjacent to A3.

A4 was the largest social group under observation, consisting of M16(D), M37(I), M11(S), M40(S), F51(D), F05(S), F13(S), and F14(S). M16 and M37 were very aggressive towards the two subordinate males, causing them to shift their attentions to the A5 group females, F42(D), F36(I), and F24(S). By late spring M37 also spent considerable time in the A5 territory and appeared to have assumed the dominant male position within this group. The satellite F49 was tolerated by members of the A4 group by now and spent increasing amounts of time within the A4 group territory. Whereas the male rabbits moved relatively freely between the A4 and A5 territories, there was no mixing by the females who kept strictly to their respective group territories. M16 associated with all the females in this group, but most commonly with F51 and F14, until his disappearance in November.

Summer 1981/82

The level of intragroup aggression between adult rabbits decreased noticeably in summer (Figure 7.3e). However, towards the end of this season when vegetation was severely depleted, especially inside the fence line, young rabbits were increasingly chased causing them to venture into new areas. This hostility which was mainly by adult female rabbits is probably a factor in reducing the high summer population to lower levels by forcing juvenile rabbits to disperse.



e Summer 1981/82

The structure of group A2 was much the same as previously with M23(D) and M46(I) remaining the only males in this group. F33 had assumed the role of dominant female and her aggression towards F52, whom she displaced, and F62 (a young rabbit) caused them to shift to the A6 and A3 group territories respectively. Another young rabbit, F64, occasionally ventured into the A2 territory from A3 but received similar treatment from F33. F69(S) was also a member of the A2 social group but regularly avoided F33, generally associating with M46. There was little aggression between M23 and M46, except when M46 ventured too close to F33. M23 would then move between them sometimes threatening M46. Despite his sub-dominant status, M46 regularly defended the A2 group territory especially from invasion by M42(D).

Membership of the A3 social group increased in summer with the addition of several young rabbits including F62 and F64. F64 subsequently moved to A6 in February.

The main changes to the A4 group in summer were the disappearance of M11 and the inclusion of two subordinate males M56 and M60. F49 was now accepted as a member of this group and assumed an intermediate status between F51(D) and F05(S). M37(D) still frequented the A4 territory although he spent more time in A5, as did M40(S). The A5 group still included F42(D), F36(I), and F24(S), as well as a young subordinate male, M59. The female hierarchy within this group was remarkably stable, with very few challenges to F42's dominant position.

Membership of the A7 group included M47 and F40. A satellite male M157 spent increasing amounts of time in the A7 territory and by late summer appeared to be accepted by the other rabbits in this group. At the same time group A6 gained F52(I), F64 and F55. M35 remained dominant in this area.

The structure of A1 and A8 was similar to the previous season with minor alterations. M42(D) ranged over both group territories and was never challenged. He usually associated with F61(D) in A1 and F53 in A8.

Autumn 1982

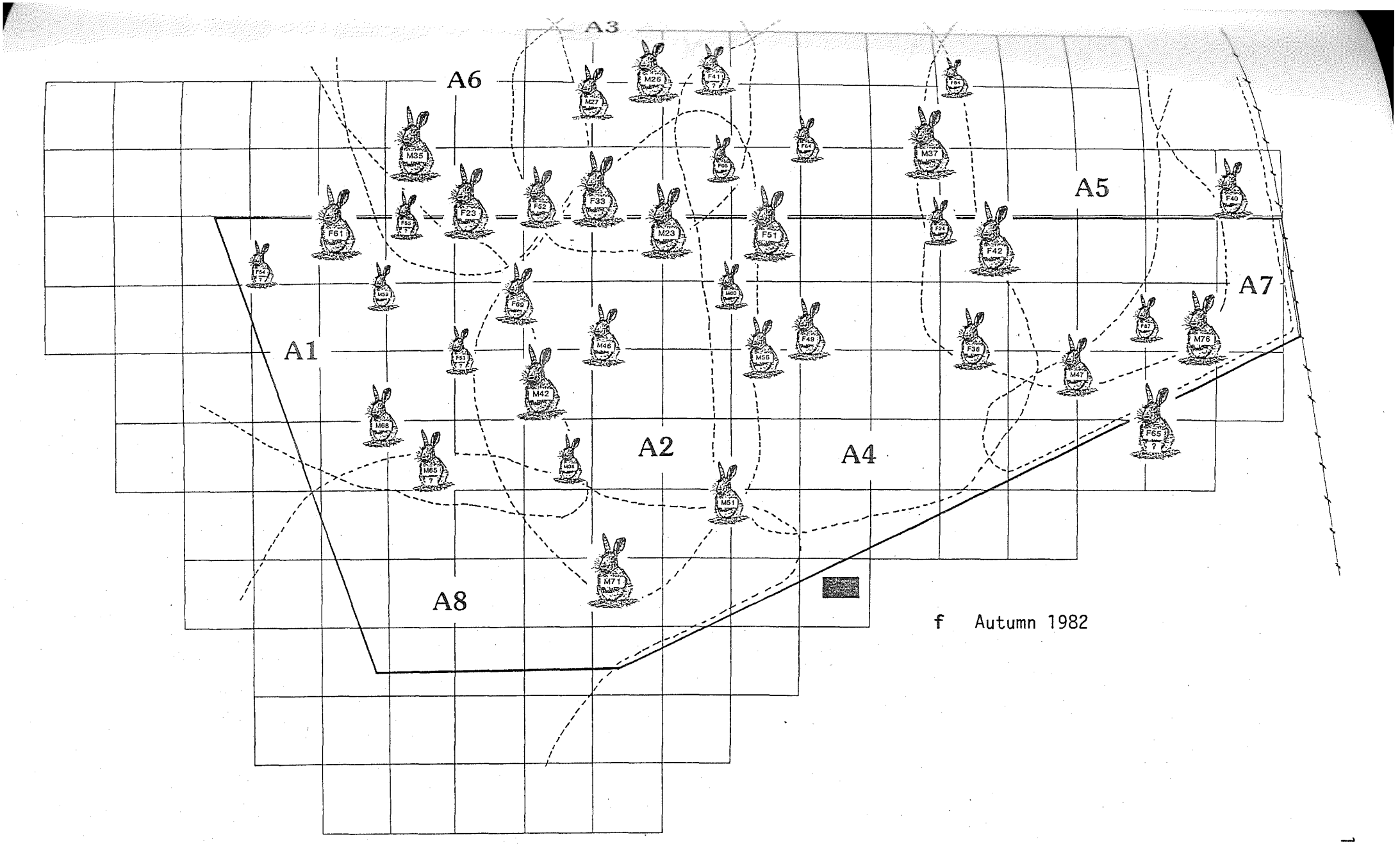
As with the previous autumn, movement was extensive and levels of territorial and aggressive behaviour were low in the early part of this season (Figure 7.3f). Rabbits from adjacent groups mixed relatively freely and seldom interacted agonistically. The main impetus for these movements was the need to forage further. Vegetation was severely depleted and rabbits were often observed browsing briar bushes and thistles, and scratching for roots. By late autumn, however, social groups were starting to reform and rabbits became more conservative in their movement patterns.

Rabbits from the A2 and A4 groups spent much time in the A3 group area where vegetation was still plentiful. Members of the A5 and A7 groups moved towards the A4 territory, especially inside the fence line, while rabbits from A1 and A8 moved into the lower parts of the A2 area. M42(D), M51(D), and M08(S) were especially far ranging, often being observed on the lower parts of the A5 territory. On several occasions M47(I) from the A7 group was seen feeding in the area between the A2 and A8 territories. Towards the end of autumn these movements ceased with an increase in the territoriality and aggressiveness of the other rabbits.

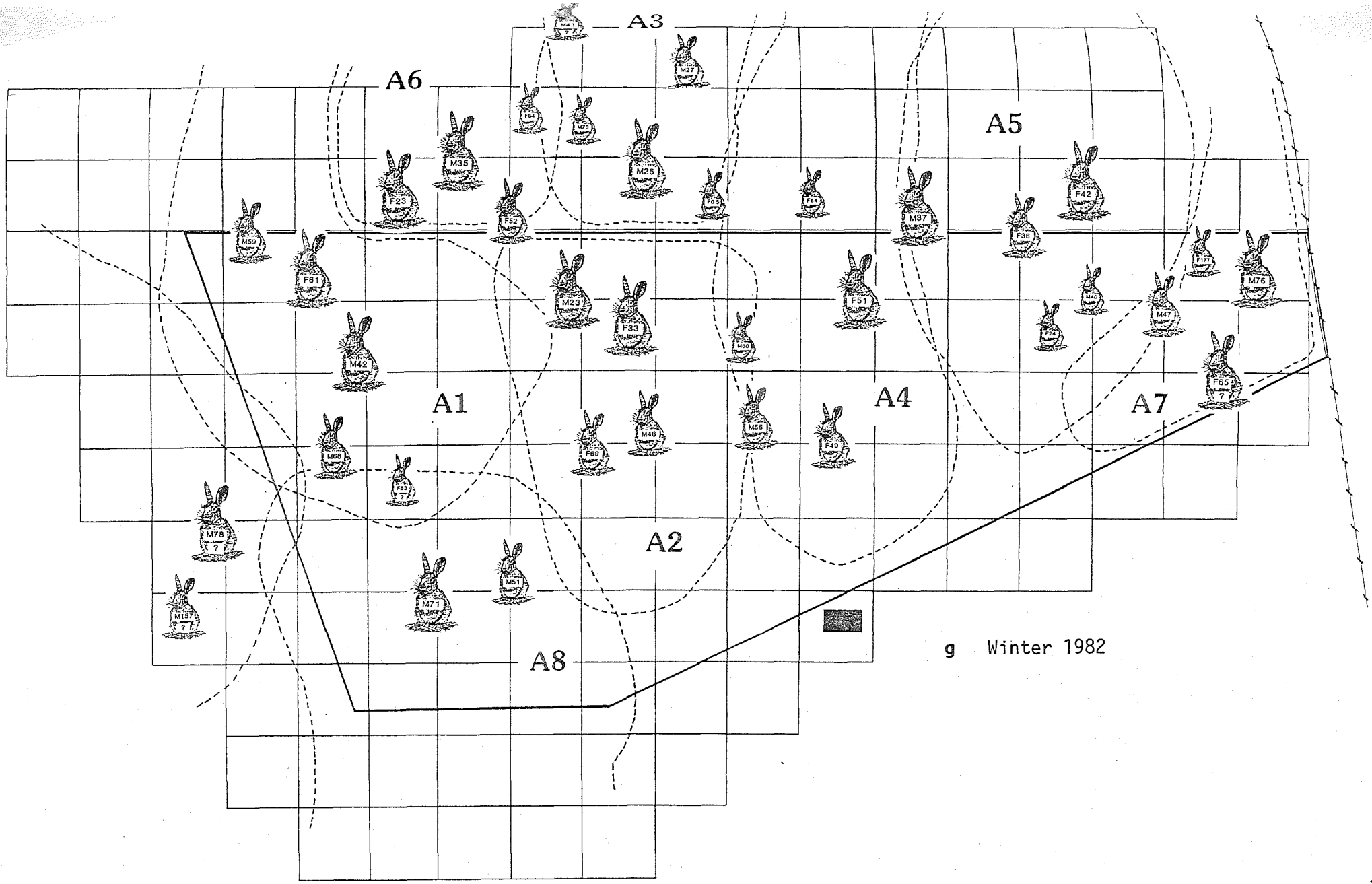
Several permanent changes occurred towards the end of autumn including F23's move to A6 and F64's move to A4. M59(S) from A5 was the target of much aggression from M37(D) and sometimes F42(D). This resulted in M59 shifting to A1 in late May/early June.

Winter 1982

Group A2 retained basically the same structure as the previous season with M23(D), M46(I), F33(D), and F69(S) (Figure 7.3g). F52(I) sometimes ventured into A2 from A6 where she spent most of her time in early winter. M23 frequently associated with her but F33 remained aggressive towards her. M56(I) and M60(S) often used part of the A2 territory but were not tolerated at close quarters by M23 and M46.



f Autumn 1982



g Winter 1982

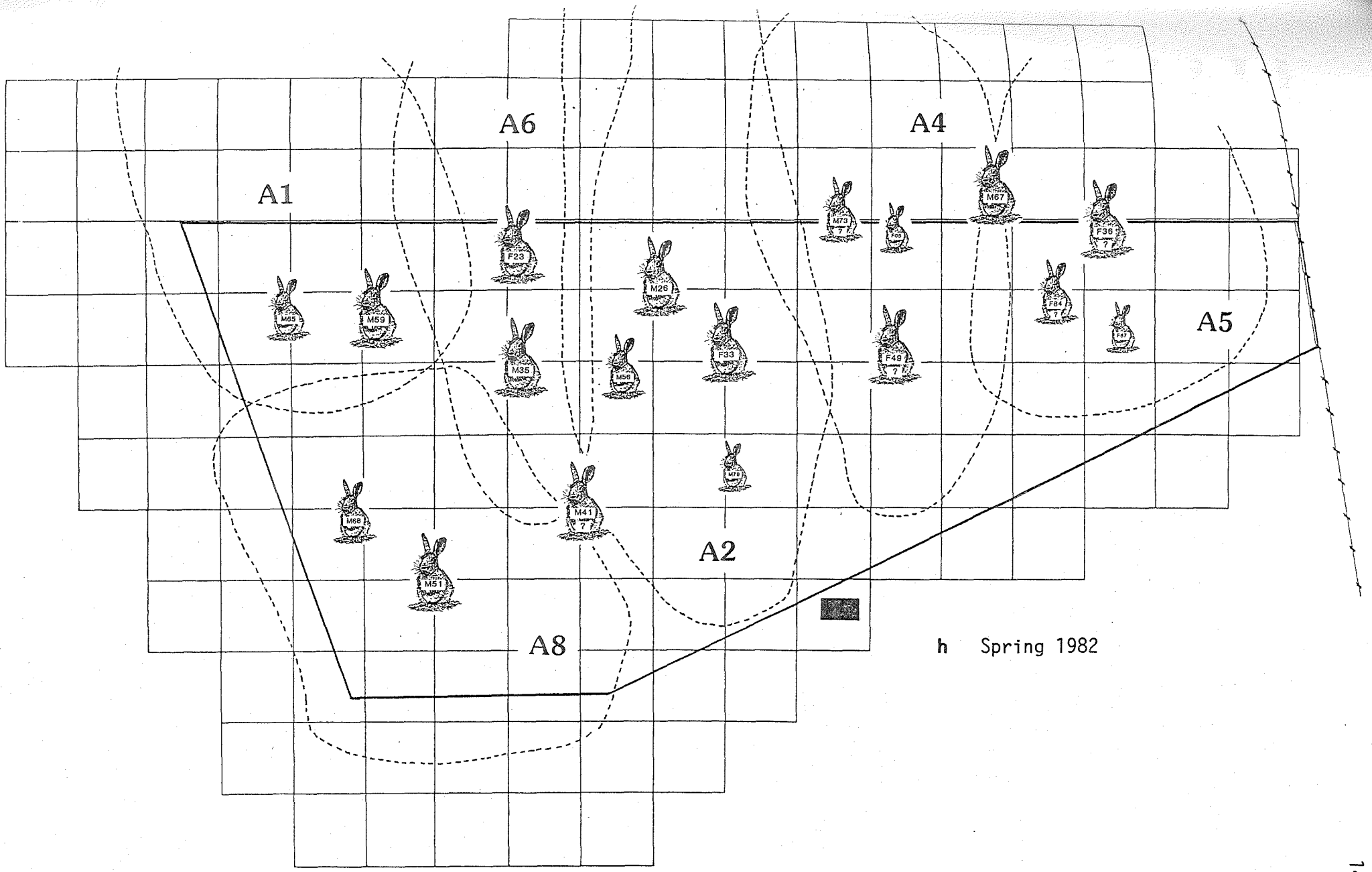
M26 remained the dominant male in A3 which also included M27(I), F05(S), and a young subordinate male, M73. M41 was a satellite who spent most of his time on the periphery of this group's territory.

M37's overall dominance of both the A4 and A5 groups appeared to continue although he spent most time in A5. A4 included M56(I) and M60(S), F51(D), F49(I), and F64(S). A5 consisted of M40(S), F42(D), F36(I), F24(S), and a young subordinate female, F84, as well as M37. There was more territorial behaviour in this area than previously, possibly because a larger number of rabbits were present. F84 was regularly harassed by the other females in the A5 group and by late winter had shifted into the A3 group territory. M37 came under increasing pressure from two males from A7, M76(D) and M47(I), who extended group A7's territory at the expense of A5's. A7 also included F177(S) and F65, who were quick to take advantage of their extended group territory.

M42(D) ceased his far ranging movements and reestablished dominance over the A1 group which also included M68(I), M59(I), and F61(D). F53 spent most of her time in A1 but sometimes ventured into the A8 territory where she was tolerated. There was very little territorial behaviour between these two groups early in winter but during August M71(D), from group A8, became highly aggressive towards males from the adjacent groups, A1 and A2. M71 was also extremely aggressive towards two other males (M157 and M78) who frequented the area immediately outside the fence line on the left side of the A1 group territory.

Spring 1982

Following the removal of many rabbits during the poison operation in August, a number of marked changes in the social organisation of the population occurred (Figure 7.3h). M26(D) immediately moved into the A2 territory with the disappearance of M23 and M46. F33 remained the dominant female in this group and, despite the decrease in population density, continued to resist F23's attempts to use the A2 area. However, two male



h Spring 1982

rabbits, M56(I) and M79(S), became incorporated into the A2 group during this period. M35(D) increased the area of the A6 group territory to include a region inside the fence line, as well as extending the A6 territory at the expense of the A3 group territory. M26 did not dispute this extension, but there were frequent aggressive encounters between M35 and, M56 and M79 from A2, and M59 from A8.

M59 became dominant in A1, as did M51 in A8 following the disappearance of M71. M41 was a satellite who used parts of the A8, A2, and A6 group territories but was regularly chased from these areas.

M67 assumed the dominant male position in A4 and A5 similar to M37's previous position. M67 had not been observed since being caught and marked in January 1982. A4 still contained F49 and F05(S), as well as M73 who had moved from A3. F49 probably assumed the dominant female role in the absence of F51 but this was never confirmed. With the disappearance of F42(D) from A5, F84(S) moved back into this social group which still included F36 as well as a young subordinate female, F87. F84's movements suggest an attraction to the social group in which an individual was born.

Most movements during this period conformed to a pattern. Following the decrease in population density, dominant males attempted to expand their group territories in all directions. However, males which had assumed a dominant position following the disappearance of the former dominant male in their group were more conservative in their actions. They appeared to merely consolidate their new status and did not extend their activity ranges appreciably. Movements of female rabbits in response to the population density change were minimal compared with males.

7.3 General Discussion

Most of the features of social organisation in rabbit populations described in previous studies (see introduction to this chapter) were observed. Rigid social group structures existed within the population for most

of the year. Despite wider ranging movements and considerable mixing of rabbits during late summer and early autumn, many associations between individuals of the same social group persisted. The attractiveness of social groups was confirmed by the continual attempts of satellite rabbits, usually males, to associate with members of established groups. Limitation of social group size and the forced dispersal of young rabbits in response to aggression from adults following the breeding season (Lockley 1961, Mykytowycz and Fullagar 1973) are two ways in which social organisation acts to reduce effective population size.

Social group size ranged from a pair of adult rabbits (group A2 during summer 1980/81) to eight adult rabbits, four males and four females (group A4 during spring 1981). The size of social groups is considered to be determined by the ability of the dominant male to maintain control over his territory (Parer 1977). The smallest groups tended to occur where the habitat was most favourable, with larger groups found in the poorer areas. Sometimes pair formation between male and female rabbits of equivalent status occurred within a social group (e.g. A2 during summer 1981/82). In other groups (e.g. A4 during spring 1981) the dominant male attempted to monopolise all the females within the group. In one or two instances a dominant male appeared to maintain a controlling influence over two adjacent groups. The sex ratio was approximately 1:1 although some groups did have a predominance of females.

Generally, social group formation is considered to be a function of the territorial conservatism (Southern 1940) and mutual attraction (Myers 1966) between female rabbits. Male rabbits then concentrate their activities in relation to the females in an attempt to maximise their reproductive success. Observations during this study suggested that while dominant males did not figure in all the matings which took place, they were successful in preventing some individuals from gaining access to females in oestrus.

Social group structure outside the breeding season appeared to be influenced by the availability of food resources. The most strongly defended

group territories during the non-breeding period coincided with the best areas of vegetation. Where vegetation was sparse, rabbits from different social groups mixed relatively freely. This suggests a relationship, at least during the non-breeding period, between the costs and benefits of defending an area. The concept of economic defendability (Brown 1964) has been demonstrated recently by Harrison (1983) for green monkeys **Cercopithecus sabaeus**. The level of aggression between different groups of green monkeys, which ranged from ritual encounters to intense fighting, was determined by the distribution and availability of food resources.

Social organisation is maintained through aggressive encounters between individuals of the same sex which lead to the formation of linear dominance hierarchies within social groups. These were evident among both males and females, whereas intersexual aggression was uncommon. Aggression between rabbits of different social groups is greatest during the breeding season when social group territories are strongly defended. In such encounters a rabbit's social status is less important than its familiarity with its surroundings (Mykytowycz et al. 1976). Dominant rabbits outside their normal ranges frequently lost aggressive encounters with intermediate and subordinate rabbits whose group territory they had invaded.

Territorial confidence is enhanced by the presence of familiar odours, derived from the submandibular and anal glands. Intergroup relationships probably rely more on olfactory communication compared with intragroup structure where visual reinforcement of relationships is more frequent. The greater degree of sociality of higher social status rabbits was confirmed by the weights of these glands for male rabbits. The inguinal glands which are associated with reproductive activity were also heavier for higher social status males. The relationship between the weights of the odoriferous glands and social status for female rabbits was not as clear, but this may have been due to recent social status changes.

The rapid changes in social organisation that occurred following the poison experiment in August 1982 reflect the opportunist nature of the rabbit. Changes began appearing just a few days after the disappearance of those rabbits that were poisoned. Together with the frequency of chinning behaviour, this suggests that olfactory information on group territory occupancy disappears quickly from the environment and that exploratory forays into neighbouring group territories are not uncommon. Daly (1979) reached similar conclusions about exploratory behaviour based on observations and mark-recapture information.

The heterogeneity of the habitat, particularly the patchiness of the food supply, appeared to influence spatial and temporal features of social organisation. The social organisation of the population was geared primarily towards reproductive efficiency and the optimal use of resources.

8 MOVEMENT AND ACTIVITY RANGE

8.1 Introduction

The term 'activity range' used in this section is almost synonymous with the more commonly used term of 'home range'. However, the movement patterns of rabbits on the study area (see below) obviated the use of home range in the strict sense. Nevertheless, the literature pertaining to home range and its methods of analysis are relevant to the results presented. Traditionally, home range has been defined as the area traversed by the individual in its normal activities of food gathering, mating, and caring for young (Burt 1943), exclusive of migrations, emigrations, or unusual erratic wanderings (Brown and Orians 1970). However, the subjective nature of classifying these latter movements, combined with a realisation of their biological importance, has led some workers to include such movements in home range records (Dice and Clark 1953, Stickel 1954, Myers and Poole 1961, Ford and Krumme 1979).

Various interpretations of the home range concept, as well as differences in the type of data dealt with, have resulted in a wide range of methods for the calculation of home range size (e.g. Hayne 1949, Calhoun and Casby 1958, Mohr and Stumpf 1966, Jennrich and Turner 1969, Schoener 1981). Many early methods of home range estimation are especially prone to sample size biases, or are based upon the assumption that observations conform to either a circular normal or bivariate normal distribution, which is rarely the case in nature (Mohr and Stumpf 1966, Metzgar 1972, 1973, Ford and Krumme 1979), especially in heterogeneous environments (van Winkle 1975). Most of these methods assume a rigid boundary for each home range, which is questionable for many species. Generally, these methods are characterised by an excessive sensitivity to the total number of records per individual and a failure to deal explicitly with the fact that not all location points are equally likely (Ford and Krumme 1979).

Frequently, areas of highest use or 'core areas' tend to be more stable, and remain more characteristic for different groups (Mohr and Stumpf 1966, Anderson 1982). This feature is reflected in the assumptions of some of the more recent home range estimation techniques (Ford and Krumme 1979, Anderson 1982), as is the premise that many animals have no fixed limits to their movements. These methods are based on the concept of a utilisation distribution (UD): the distribution that describes the proportion of time an animal spends at each particular point. Since UD's were first suggested by Hayne (1949) several workers have attempted to develop techniques for measuring home ranges from such distributions. Whereas early methods (e.g. Calhoun and Casby 1958, Jennrich and Turner 1969) suffer from restrictions due to assumptions on the shape of the distributions, more recent methods (Ford and Krumme 1979, Dixon and Chapman 1980, Anderson 1982) enable calculation of home range areas irrespective of the shape of the UD.

Paralleling the development of these UD techniques has been the acceptance of a more flexible definition of home range. Home range is now often understood to be the area of the smallest sub-region of an animal's UD which accounts for a specified proportion (e.g. 80% or 95%) of its total utilisation (Jennrich and Turner 1969, van Winkle 1975, Anderson 1982). Such methods are better suited to examinations of the way in which activity is distributed within home ranges and descriptions of resource utilisation.

There is considerable variation among previously reported home range estimates for the rabbit (e.g. Myers and Poole 1959, 1961, Gibb et al. 1978, Henderson 1979, Fullagar 1981). Some of these results are from enclosure studies while others are from observations or trapping of natural populations. Similar variation is found in the literature on home range estimates for the eastern cottontail **Sylvilagus floridanus mearnsii** (e.g. Allen 1939, Schwartz 1941, Haugen 1942). Methodology accounts for much of this variation since it has long been recognised that major differences exist between trap-revealed ranges and true home ranges (Hayne 1949, Stickel 1954, Sanderson 1966, Brown

and Orians 1970).

Although true variation does occur, home ranges in rabbits are relatively stable. Adult rabbits are sedentary (Southern 1940, Tyndale-Biscoe and Williams 1955, Myers and Schneider 1964, Mykytowycz and Gambale 1965) and apart from small changes, actual shifts of home range are rare (Myers and Poole 1961, Dunsmore 1974, Gibb et al. 1978, Daly 1979). In fact, most home range shifts can be classified as dispersal movements and usually occur before rabbits reach sexual maturity (Mykytowycz 1960, Myers and Poole 1961, Mykytowycz and Gambale 1965, Daly 1979).

Movement patterns and consequent home ranges for rabbits in this study differed from the normal situation. This arises because a considerable proportion of the population were not typical warren or burrow dwellers. The nature of the habitat was not conducive to the formation of warren systems, mainly because of the unsuitability of the substrate for burrowing. Consequently, many rabbits had their usual resting locations in the rocky outcrops outside the observed area (as outlined in section 3.2.1). Therefore, observations on all but a few individuals, who were permanently resident within the observed area, only comprised the activity range of rabbits during the peak period of activity. Records for resident rabbits conformed closer to the concept of home range although information on nocturnal movements is not included.

Several features of the rabbits' movement patterns and activity ranges were examined including activity range size and shape, and the nature of any changes which occurred during the study. Information on these aspects provided a base for comparisons with rabbits studied under more 'typical' conditions (e.g. Southern 1940, Dunsmore 1974, Gibb et al. 1978, Daly 1979).

8.2 Results and Discussion

Only transect sampling data were used for the calculation of activity ranges and movement patterns. These data covered a larger number of

individuals and a greater time span than focal animal sampling data.

8.2.1 Comparison of methods

A small, representative sample of rabbits was chosen from which comparisons of various range estimation methods could be made. These methods included the minimum convex polygon (MCP), observed range length, Jennrich and Turner's (1969) matrix determinant method, and a non-parametric technique (Anderson 1982).

The simplest method (MCP) involves drawing the smallest convex polygon which contains all the observation points for an individual and taking the enclosed area as the animal's activity range. This area is calculated using the mapmaker's formula:

$$MCP = \tfrac{1}{2} \sum_{i=1}^{n} (x_i y_{i+1} - x_{i+1} y_i)$$

The vertices of the polygon are ordered (clockwise or counter-clockwise) around their geographic centre. The point (x_i, y_i) is the ith ordered vertex from a total of n points and $(x_{n+1}, y_{n+1}) = (x_1, y_1)$.

Observed range length is the distance between the most widely separated location points. This value is sometimes modified to include the addition of a constant as in the boundary strip method (Stickel 1954). Such adjustments to range lengths are more important in trapping studies where distances between traps are relatively large in comparison with the location points for observation records.

Jennrich and Turner's (1969) method is based on the determinant of the covariance matrix of the location points and is given by the formula:

$$\text{Area} = 6 \text{ pi } [S]^{\frac{1}{2}}$$

Here [S] is the determinant of the location point covariance matrix,

$$S = \begin{pmatrix} s_{xx} & s_{xy} \\ s_{yx} & s_{yy} \end{pmatrix}$$

defined by the equations:

$$s_{xx} = \frac{1}{n-2} \sum_{i=1}^{n} (x_i - x)^2 \qquad s_{yy} = \frac{1}{n-2} \sum_{i=1}^{n} (y_i - y)^2$$

$$s_{xy} = s_{yx} = \frac{1}{n-2} \sum_{i=1}^{n} (x_i - x)(y_i - y)$$

$$x = \frac{1}{n} \sum_{i=1}^{n} x_i \qquad y = \frac{1}{n} \sum_{i=1}^{n} y_i$$

Jennrich and Turner defined home range as the smallest region which accounts for 95% of an animal's utilisation of its habitat. If the constant '6' is replaced by '9', the resulting area accounts for 99% of an animal's utilisation of its environment. This technique is very similar to Calhoun and Casby's (1958) method based on recapture radii, but is designed to measure non-circular (elliptical) as well as circular ranges.

Finally, the non-parametric technique describes home range in a probabilistic sense and makes no assumption about the shape of the underlying UD. It is based on a Fourier transform of the UD, allows for fine resolution of the estimated density function, and produces an estimate that is close to the 'true' distribution (Anderson 1982). Estimates from this method are called MAP values, an abbreviation for minimum area vs. probability. For example, MAP(0.95) is the smallest area which accounts for 95% of an animal's space utilisation.

Results of the above methods of activity range estimation are compared in Table 8.1. The data included in this comparison are from a representative sample of rabbits (a male and female rabbit of each social status are included). Several examples of seasonal activity range data are shown in Figure 8.1 to illustrate the biases associated with some of these methods.

Observed range length has been used as an index of home range size in a number of studies (e.g. Fitzgerald et al. 1981, Read 1984). However, examination of Table 8.1 and Figure 8.1 illustrates the insensitivity of this measure in relation to major differences between individuals' activity ranges.

Table 8.1 Results of several methods of home range estimation from a representative sample of rabbits.

Rabbit	Season	Number of observations	Home range size (ha) MCP	J&T	MAP (0.95)	Observed range length (m)
F05	Spr 81	52	0.80	0.71	0.30	134.2
	Win 82	72	0.92	0.71	0.28	161.6
	Spr 82	67	0.93	1.06	0.51	138.3
F33	Sum 81/82	49	0.63	0.58	0.28	114.2
	Aut 82	72	0.59	0.61	0.13	106.1
	Win 82	82	0.74	0.73	0.31	115.6
	Spr 82	107	1.06	0.68	0.36	135.8
F49	Spr 81	55	0.86	0.72	0.25	154.4
	Sum 81/82	28	1.05	1.15	0.37	147.7
	Win 82	43	0.81	0.88	0.39	117.2
	Spr 82	58	0.97	1.39	0.68	142.3
M23	Win 81	104	0.45	0.26	0.06	109.2
	Spr 81	103	0.93	0.37	0.09	191.0
	Sum 81/82	58	0.36	0.27	0.10	84.9
	Aut 82	54	0.66	0.74	0.14	141.5
	Win 82	159	0.73	0.57	0.19	120.9
M37	Win 81	47	1.73	1.36	0.35	223.0
	Spr 81	68	0.90	0.81	0.41	162.3
	Sum 81/82	33	0.41	0.48	0.23	87.5
	Aut 82	48	0.57	0.38	0.11	123.7
	Win 82	91	1.00	0.72	0.22	167.7
M40	Aut 82	37	0.90	1.48	0.37	171.0
	Win 82	84	1.14	1.00	0.56	185.5
	Mean:		0.83	0.77	0.29	140.7
	Standard deviation:		0.29	0.34	0.16	33.6
	Coeff. of variation (%):		35	44	55	24

MCP = minimum convex polygon, J&T = Jennrich and Turner's matrix method, MAP(0.95) = Anderson's non-parametric estimate

Whereas the basic utilisation distributions for M23 were similar in spring 1981 and summer 1981/82 (Figure 8.1a and b), the presence of two outlying observations in the spring data result in a deceptively high observed range length (191.0 m). When these two location points are excluded, the resulting range length (100.6 m) is much closer to the value for summer (84.9 m). The

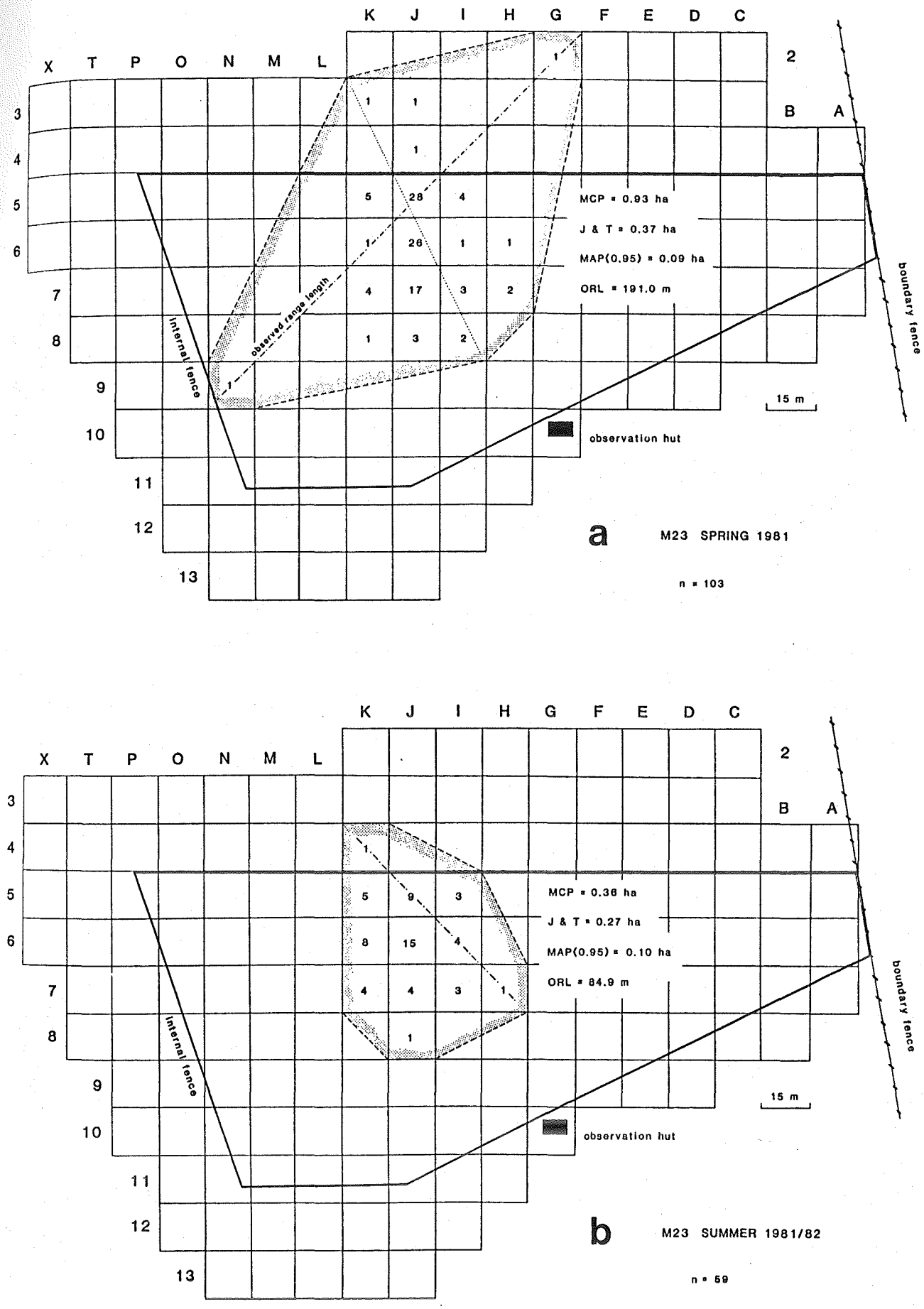
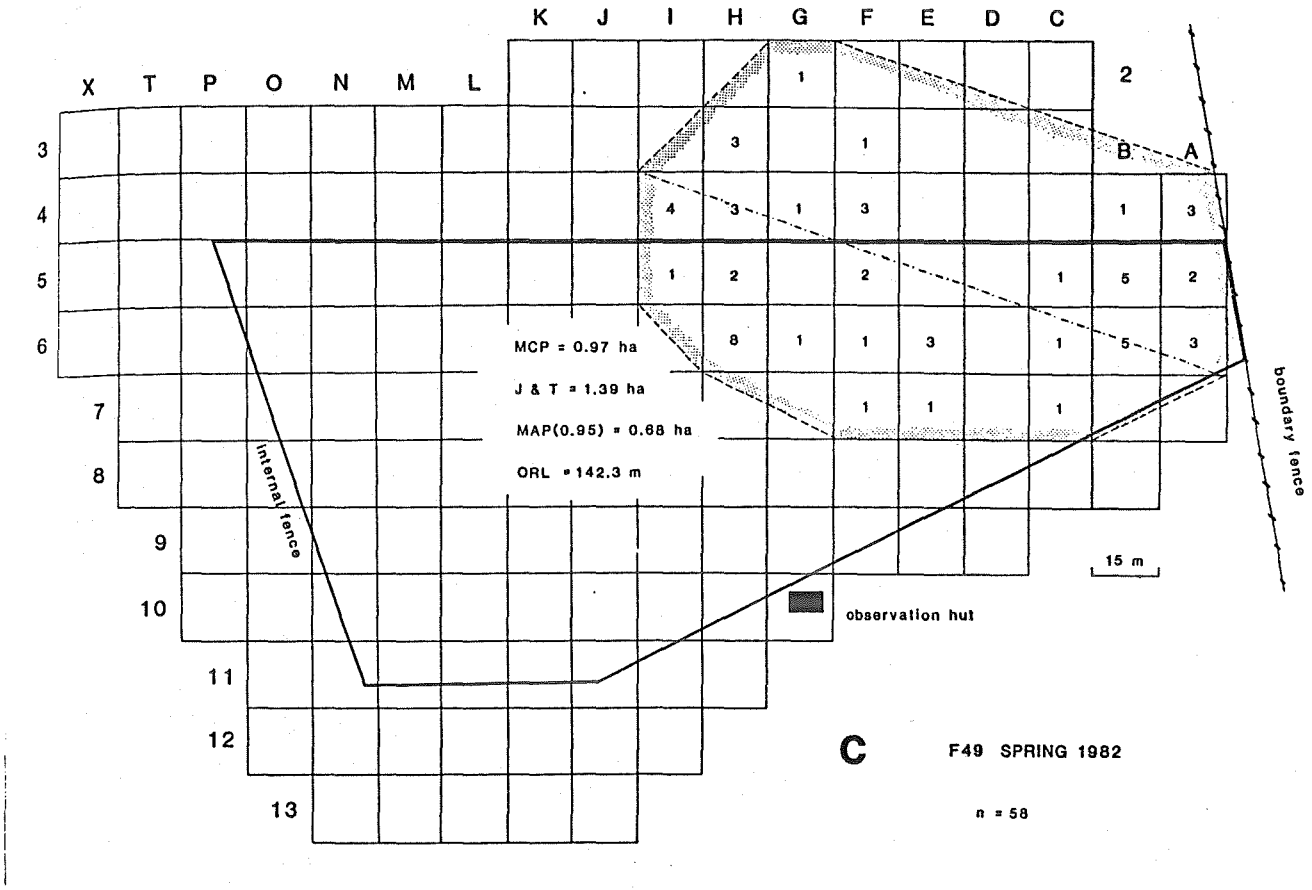


Figure 8.1 (a-c) Activity range details illustrating the wide variation in estimates of size between the various methods (MCP = minimum convex polygon, J & T = Jennrich and Turner's matrix determinant method, MAP(0.95) = Anderson's non-parametric estimate, ORL = observed range length).


K J I H G F E D C
X T P O N M L
2
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B A
1
3 1
4 3 1 3 1 3
1 2 2 1 5 2
8 1 1 3 1 5 3
1 1 1
MCP = 0.97 ha
J & T = 1.39 ha
MAP(0.95) = 0.68 ha
ORL = 142.3 m
internal fence
boundary fence
15 m
observation hut
C
F49 SPRING 1982
n = 58

similarity of the UD's for these two seasons is then also reflected in the similar orientation of the range length axes.

MCP calculations are similarly affected by outlying data points. Inspection of the same data for M23 reveals that from these two similar UD's, the resulting MCP estimate for spring is almost three times that for summer. In fact, almost 95% of the observations in spring fall within just 29% of the calculated MCP areas (cf. 56% for summer). Although MCP estimates for M23 in spring 1981 (0.93 ha) and F49 in spring 1982 (0.97 ha) are similar, the underlying patterns of space utilisation for these two rabbits differ markedly (Figure 8.1a and c).

While the Jennrich and Turner matrix determinant method does not mask differences between UD's as severely as the previous two methods, it nevertheless has serious disadvantages. Because it is based on location point radii from the calculated geographic centre of activity, it is overly sensitive to UD's with a large proportion of location records near the edge of the animal's range, as with F49 in spring 1982. The value obtained with this method (1.39 ha) exceeds even the MCP estimate (0.97 ha). The matrix determinant technique would result in gross overestimates if used for calculating home range size for species which regularly patrol their range boundaries (e.g. many carnivores).

The most suitable technique for estimating the size of activity ranges was Anderson's (1982) Fourier transform method. In all cases MAP(0.95) values were considerably less than the corresponding Jennrich and Turner (95% of range) or MCP (100% of range) estimates. Closer inspection of the UD's in Figure 8.1 reveals that MAP estimates result in values that are very similar to the actual distribution. The MAP(0.95) estimate of 0.09 ha for M23's spring 1981 activity range corresponds to exactly four grid squares (each grid square equals 0.0225 ha). The four grid squares with the highest intensity of activity actually contain 74% of the spring observations. The variation between the actual distribution and the estimate from the smoothed utilisation

distribution is due largely to the smoothing process. In addition, MAP values that comprise a small number of grid squares are less accurate because of internal constraints on the computer program used to analyse the data (D J Anderson pers. comm.). Fortunately, most rabbits ranged over wider areas than M23 so this factor did not interfere greatly with accuracy.

As a corollary to the visual comparison of these techniques, the coefficients of variation for activity range estimates (see Table 8.1) indicate that MAP values are best for preserving the natural variation between individual activity ranges. The considerably lower coefficient of variation for observed range length is not unexpected as range length is a linear (one-dimensional) measure compared with areal (two-dimensional) measures for the other methods.

8.2.2 Sample size

Another important factor to be considered for activity range analyses was the size of the data sets to be included. As the number of observations increases, the size of the area accounted for increases until a point is reached where continued observation results in little or no increase to the area (Figure 8.2). The concept behind such 'observation-area' curves was adapted from 'species-area' curves (Odum and Keunzler 1955). These curves conform to the formula:

$$A = cN^z$$

where A = activity (or home) range area,

c = a constant,

N = the number of location records, and

z = the slope of the line relating log A and log N.

Most rabbits have activity patterns that show very little daily variation and, in fact, month to month range adjustments are generally insignificant. Resulting observation-area curves are smooth as for M23's summer 1981/82 data (Figure 8.2a). Partial changes in an animal's space utilisation result in the

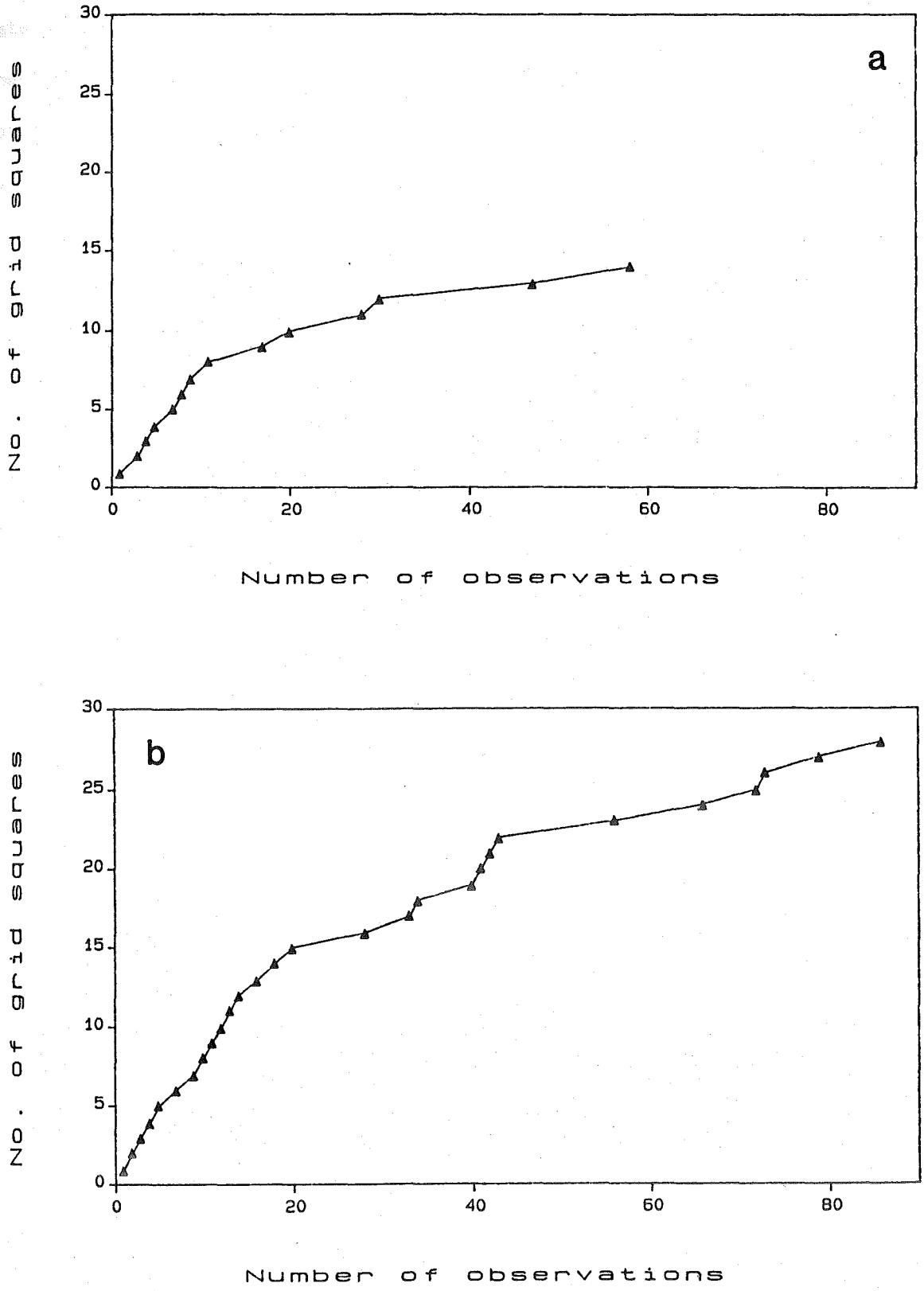


Figure 8.2 Observation-area curves for (a) M23's summer 1981/82 activity range and (b) M37's winter 1981 activity range.

observation-area curve having a 'stepped' appearance, as for M37's winter 1981 data (Figure 8.2b), but this was not common. Ables (1969) found that some of the foxes **Vulpes vulpes** he studied had such stepped curves, caused by patterns of daily use where different portions of the range were used on successive days.

By applying a logarithmic transformation to the observation-area curve equation and solving for various levels of increase (z), the number of observations required to reach these levels can be found. For example, the 1% level represents a point where the addition of an extra observation adds less than 1% to the total area. Using the same sample of rabbits as for Table 8.1, a series of values were found for three levels of increase, 1%, 2%, and 5% (Table 8.2).

Table 8.2 Number of observations required to reach the 1%, 2%, and 5% levels of increase for a representative sample of rabbits.

Category	n	Mean number of observations (and range) 1%	2%	5%
Seasons:				
Males	11	67.6 (58-78)	33.7 (29-39)	13.5 (12-16)
Females	11	73.9 (62-84)	37.0 (31-42)	14.7 (12-17)
Months:				
Males	32	77.8 (37-123)	38.6 (19-62)	15.4 (7-25)
Females	23	77.9 (58-95)	39.0 (31-47)	15.7 (13-19)

n = sample size

There was very little difference both between the sexes and for monthly records compared with seasonal records. The 2% level was chosen to give reliability to range size estimation. Accordingly, only data sets with more than 40 observations were included in activity range analyses. The narrow range of the number of observations required at each level of increase for

seasonal records supports the use of a cut-off point of 40 observations for data inclusion. Ranges were greater for monthly records but as these values are calculated by regression, the smaller size of monthly data sets may be responsible.

Calculation of area for these curves was done by summation of the grid squares used for any given number of observations, rather than using one of the range size estimation techniques described above. This eliminates the problem of outlying observation records causing large fluctuations in area values as well as observations within the boundaries of previous records contributing no increase to area. This technique is similar to the cell method described by Rhoades and Langham (1984).

The relationship between the number of observations and the area they account for is partially dependent on the scale of the grid system used (or in the case of trapping studies the distance between adjacent traps). The finer the grid system, the more observations are required to reach a particular level of increase. However, this constraint is offset by the increased accuracy conferred on range estimates by using a finer grid system.

Odum and Keunzler (1955) found that the number of observations required to reach the 1% level for three species of birds they studied ranged from 25 to 90. However, their areal values were obtained from MCP calculations which would undoubtedly lead to the type of variation mentioned above. Fitzgerald et al. (1981) found that range lengths and areas for mice **Mus musculus** in a forest habitat stabilised with about 25 records. Haugen (1942) used records with nine or more captures to determine home range size for cottontails. Although this seems low, the trap interval used was 110 yards, effectively meaning that the area associated with each trap was 2.5 acres (approx. 1 ha). A similar trap interval (115 m) was used by Dolbeer and Clark (1975) in a study of snowshoe hares. Estimated home range sizes reached an apparent asymptotic value after 20 recaptures, confirming the wider range of movement of hares in comparison with other lagomorphs.

8.2.3 Activity range shape

The shape of the rabbits' UD's were influenced by, but not entirely dependent upon, food resources and topographical features. The distribution of preferred plant species influenced the rabbits' movement patterns to some extent. This was especially noticeable in spring months when most vegetation growth occurred, including a flush of succulent daisy, a highly palatable species. Another important factor was the presence of conspecifics. This behavioural factor was especially true during the breeding season when social interaction was greatest, and dominant individuals often restricted the movements of rabbits of lower social status. Such constraints were generally in relation to the presence of females, so a dominant male's 'sphere of influence' tended to shift in relation to the movement patterns of particular females rather than be restricted to one location. Myers and Poole (1961) recorded behavioural interactions with conspecifics as an important determinant of home range size and shape in their enclosure studies.

During the early part of the study, excessive trapping created a temporary 'fence-effect' (see section 9.2). This resulted in a higher number of rabbits outside the fenced area and some spreading of activity ranges along the fence margin, especially among females. Following changes in the trapping regime, the number of rabbits using the area inside the fence line increased and the shape of activity ranges was restored to something like the original pattern.

The effect of habitat was probably most noticeable for the few rabbits who were resident within the fenced area. For example the shape of M23's and F33's activity (and home) ranges was influenced by the presence of a small gully around which they concentrated their activities. In fact, M23 and F33 used several burrows within the gully as their permanent resting locations. Their activities tended to fall within an elongated UD focussed on this gully, which provided a nearby refuge following disturbances (Figure 8.3). Also, plant growth was greater around the gully, obviously adding to the

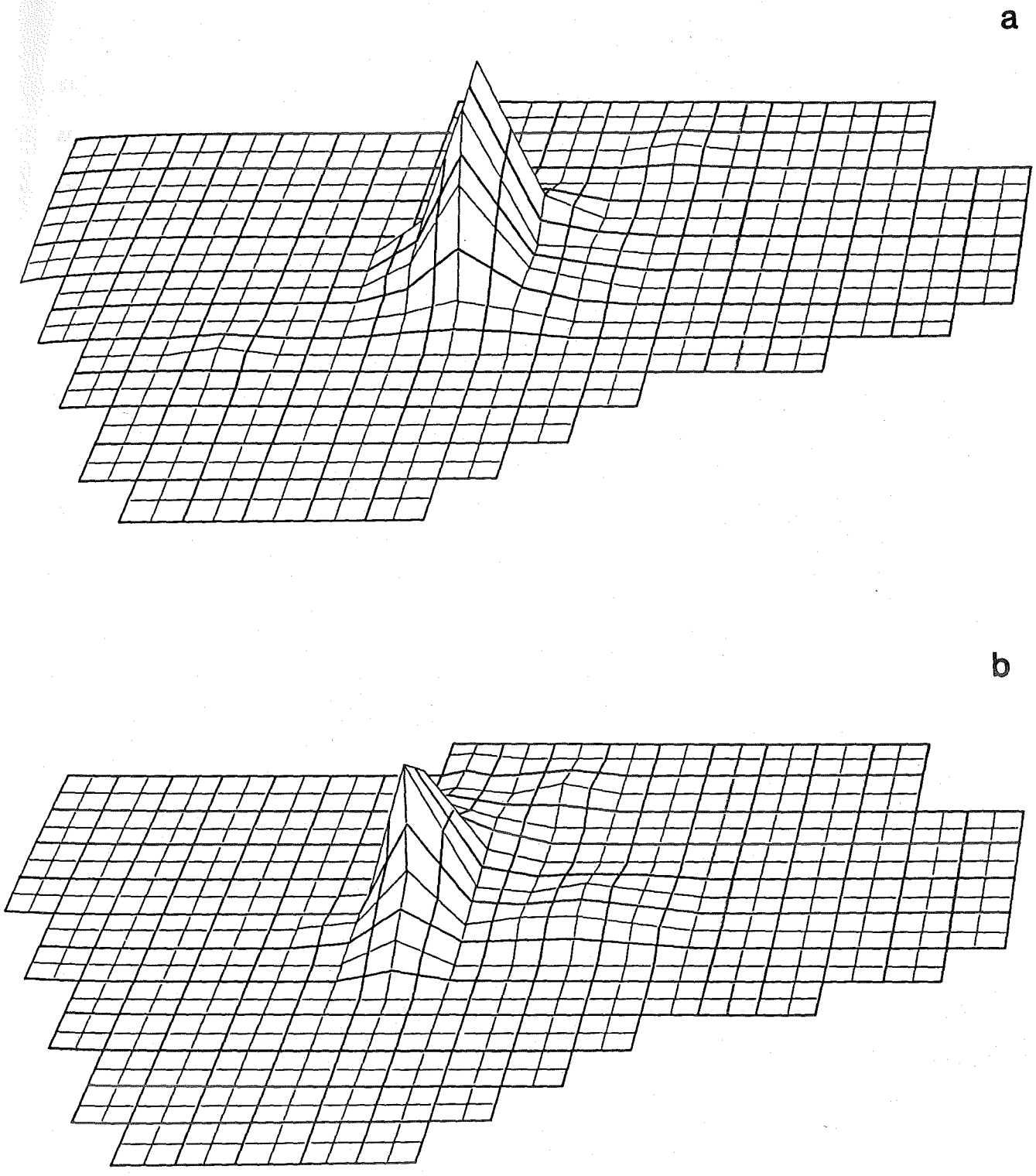


Figure 8.3 Utilisation distributions for (a) M23 and (b) F33 in spring 1981.

favourability of this area. Behaviour observations suggested that this was probably the most strongly defended zone within the study area.

The total (or home) range for most of the rabbits observed during this study differed from the previously recorded pattern for rabbits. Rabbits' activities are generally focussed around a burrow or warren system where most feeding and social activities occur (Southern 1940, Thompson and Worden 1956, Fullagar 1981). On the Butchers Dam study area vegetation was extremely sparse among the rocky outcrops where the majority of rabbits had their resting locations. Following emergence from these resting locations each day, the rabbits had to move up to 100 m to their activity or feeding ranges. The resulting home ranges were therefore comprised of two core areas, one for resting and one for feeding and other activities, connected by a narrow path over which these daily movements occurred. Considerable movements to feeding areas have also been reported elsewhere (Gibb et al. 1978) especially during times of food shortage.

8.2.4 Activity range size

MAP(0.80) values (i.e. the minimum area containing 80% of an individual's observations) were chosen for activity range comparisons for a number of reasons. Particularly important was the fact that higher MAP values (e.g. 0.95 or 0.99) are less accurate. This arises because a very small number of observations in the 'tails' of a rabbit's UD can have a large effect on the total area calculated, and therefore confidence limits for high MAP values are large. Consequently, MAP(0.80) estimates were better suited for comparisons between the sexes, levels of social status, and seasons. Gibb et al. (1978) used a "concentric band" method of estimating home range area and also found that 80% ranges were more reliable than those containing 90% or 95% of sightings.

The mean activity range size (±s.e.) for the total sample was 0.20±0.016 ha. Although an analysis of variance (Table 8.3) gave no significant

Table 8.3 Analysis of variance for MAP(0.80) values.

Source of variation	df	Sum of squares	Mean squares	F	p
Sex	1	.02035	.02035	1.13	0.29
Social status	2	.02728	.01364	0.76	0.47
Season	3	.08770	.02923	1.63	0.19
Sex x status	2	.00855	.00427	0.24	0.79
Sex x season	3	.10964	.03654	2.04	0.11
Status x season	6	.22937	.03822	2.13	0.06
Sex x status x season	6	.04868	.00811	0.45	0.84
Error	62	1.1120			
Total	85	1.7369			

differences, several trends were evident. Male rabbits had smaller ranges (0.19±0.020 ha) than females (0.23±0.021 ha), although this difference was not significant. Initially it was thought that biases within the sample with respect to particular social status ranks or seasons may have produced this result. However, closer examination of the data revealed that females of all social status ranks had larger MAP(0.80) activity ranges than male rabbits of the corresponding rank, although the difference for subordinate individuals was very small (Table 8.4). Also, dominant males had smaller ranges than intermediates or subordinates, but little variation existed among females of different social status.

Previous research has indicated that male rabbits have larger home ranges than females (Myers and Poole 1961, Gibb et al. 1978, Fullagar 1981). This is also the case for several other lagomorph species including cottontails (Haugen 1942), brush rabbits **Sylvilagus bachmani** (Shields 1960), and hares (Douglas 1970). The main difference between these studies and the present one is the restriction of observations in this study to a particular activity period. Consequently, activity range measurements are indicative of an individual's utilisation of the food resource, although in the case of males during the breeding season this resource-base is extended to include oestrous

Table 8.4 Mean MAP(0.80) values (ha) for rabbits of different social status, sample size in brackets.

Sex	Social status rank Dominant	Intermediate	Subordinate	Total
Male	.15 (22)	.17 (17)	.24 (8)	0.19
Female	.22 (17)	.21 (11)	.25 (10)	0.23

females (Russell 1984). Pielowski (1972) found that during the breeding season male hares concentrated their activities in a small area, probably determined by the movements of females in oestrus.

The habitat in this study was probably more heterogeneous than in those mentioned above, especially the enclosure studies of Myers and Poole (1961) and Gibb et al. (1978). Consequently, the movement patterns of male rabbits were influenced more by the quality of the habitat (and during part of the year its favourability for females in oestrus), rather than the quantity. Therefore, it is not surprising to find that rabbits of higher social status occupy smaller activity ranges as essentially they were able to control the 'best' areas in terms of resources. Similarly, Allen (1939) reports that in a population of cottontails in an heterogeneous habitat, the most favourably located individuals in terms of food supply and cover, had the smallest ranges. Gibb et al. (1978) reported that older and presumably more dominant individuals inhabited smaller ranges than younger rabbits, and that they also survived better particularly at high density. McNab (1963) confirms that food supply is an important determinant of home range size for a wide range of mammal species.

MAP(0.80) activity ranges were generally smaller in autumn (0.17±0.042 ha) than during other seasons but there were insufficient data to test the significance of this difference. The largest activity ranges were found in spring (0.23±0.022 ha) and summer (0.24±0.081 ha) when most breeding activity

occurred. In their enclosure studies, Myers and Poole (1961) noted a marked seasonal decrease in home range size during the breeding season when territorial behaviour was at its height; this seasonal difference occurred at all population densities. However, this was not reflected in home range areas for rabbits in the Kourarau enclosure (Wairarapa, North Island) where both male and female home ranges were largest in spring (Gibb et al. 1978). This variation between results of different studies points to a complex of factors influencing home or activity range size in rabbits, including population density, food quality, and the heterogeneity of the environment.

A marked change in activity range size occurred following the poison operation in August 1982 (Table 8.5). Increases in activity range were recorded for dominant and intermediate status rabbits of both sexes. Subordinate females were the only group to show a decrease in range size while there were insufficient data for subordinate males to calculate a value for spring 1982. The decrease shown by subordinate females may have been due to the records of two individuals, F84 and F87, who had very small activity ranges and had not been included in the winter calculations. Another subordinate female, F05, who had 72 and 67 observations in winter and spring respectively did show the expected increase. F05's activity range increased from 0.20 ha to 0.36 ha following the poisoning operation.

The most likely explanation for these changes is the response to a decrease in population density due to the rabbits killed during the poison operation. This led to a series of social group and activity range adjustments among the survivors in response to the increased space available (see section 7.2.5). In fact, only two rabbits, F23 and F36, decreased their activity range size over this period. During the same period F36's social status changed from intermediate to dominant with the death of the previous dominant female (F42) in her social group. Therefore, a decrease in F36's activity range is not entirely inconsistent with the other results when the change in social status is taken into account. Similar changes in home range size in response to

Table 8.5 MAP(0.80) activity range size (ha) before (winter) and following (spring) the poison operation in August 1982.

Season	Males			Females		
	Dom	Int	Sub	Dom	Int	Sub
Winter 1982	.13	.18	.30	.14	.29	.34
Spring 1982	.24	.33	-	.19	.41	.22

Dom = dominant, Int = intermediate, Sub = subordinate

population density have been reported elsewhere for rabbits (Myers and Poole 1959, 1961, Gibb et al. 1978) and hares (Pielowski 1972).

No information on night ranges was collected although mark-recapture results do provide some indirect evidence to support previous findings which indicate that night ranges are larger than day ranges (Gibb et al. 1978). On several occasions rabbits were captured in traps outside the range within which they had previously been observed, indicating that a wider range of movement does occur at night. In addition, two marked rabbits (F41 and F66) that were killed during the poison operation in August 1982 did not have observed activity ranges within the observed area, where all the poison baits were laid. F41 had only been observed seven times in the previous five months, each time on the outer margin of the gridded area; F66 had last been seen in March 1982. This suggests that their night ranges were larger than their day ranges and included part of the observed area.

8.2.5 Activity range shifts

Before shifts of activity range could be examined, a reliable method of pin-pointing the rabbits' activities each month had to be found. There were two techniques available, the geographic centre of activity and the activity peak. The centre of activity method simply calculates the arithmetic mean of the coordinates of the all the grid points at which a rabbit is observed, and

therefore takes all observations into account. The activity peak is the point of highest frequency (mode) of the rabbit's activities, and as such is not dependent on the entire set of location points for a particular month. Results from these two methods were compared (Table 8.6).

Table 8.6 Variation between geographic centre of activity and activity peak locations for a representative sample of rabbits.

Rabbit	Social status	n	Mean difference (m)
F33	Dom	7	11.7
F49	Int	3	23.0
F05	Sub	3	20.4
M23	Dom	13	7.4
M37	Int	7	14.7
M40	Sub	2	15.5

Dom = dominant, Int = intermediate, Sub = subordinate, n = sample size

The difference between the two techniques is not great. For each sex, both methods show the least variation for dominant rabbits, while the variation for intermediate and subordinate individuals is approximately twice that for dominants. The two dominant individuals, M23 and F33, were also resident within the observed area and this fact could have contributed to the difference. Their ranges were extremely stable over the duration of the study. The overall (unweighted) mean difference between these two methods was 12.6 m, which was not considered large enough in relation to the grid size used to preclude either method from being used.

For convenience the geographic centre of activity was chosen and all individuals with at least 10 observations for the month were included. Several trends were evident (Table 8.7). There was little difference between the mean shift distance for males (15.7 m) and females (18.1 m). However, when social

Table 8.7 Analysis of variance for monthly shifts of activity range.

Source of variation	df	Sum of squares	Mean squares	F	p
Sex	1	254.04	254.04	1.54	0.21
Social status	2	3194.61	714.36	4.33	0.01
Season	3	1428.72	1064.87	6.46	0.00
Sex x status	2	1438.41	719.21	4.36	0.01
Sex x season	3	1602.42	534.14	3.24	0.02
Status x season	6	2222.66	370.44	2.25	0.04
Sex x status x season	6	1181.38	196.90	1.19	0.31
Error	227	37437.31	164.92		
Total	250	49007.68	196.03		

Table 8.8 Mean monthly shifts of activity range (m) for rabbits of different social status, sample size in brackets.

	Social status rank			
Sex	Dominant	Intermediate	Subordinate	Total
Males	9.3 (56)	15.1 (50)	22.7 (22)	15.7 (128)
Females	18.9 (47)	15.7 (49)	19.5 (27)	18.1 (125)

status was taken into account, it became apparent that dominant males were considerably more sedentary than other groups in the population (Duncan's new multiple range test, $p<.05$) (Table 8.8). This confirms the results above, namely that dominant individuals are more likely to concentrate their activities in the most ideal areas. As a consequence, intermediate and subordinate rabbits are forced to shift their activities more frequently in order to gain access to sufficient food resources. Figure 8.4 illustrates these results for male and female rabbits of each social status.

Seasonal trends revealed different patterns for male and female rabbits (Table 8.9). Activity range shifts in winter were small for both sexes, but increased noticeably in spring when vegetation growth and the increased social

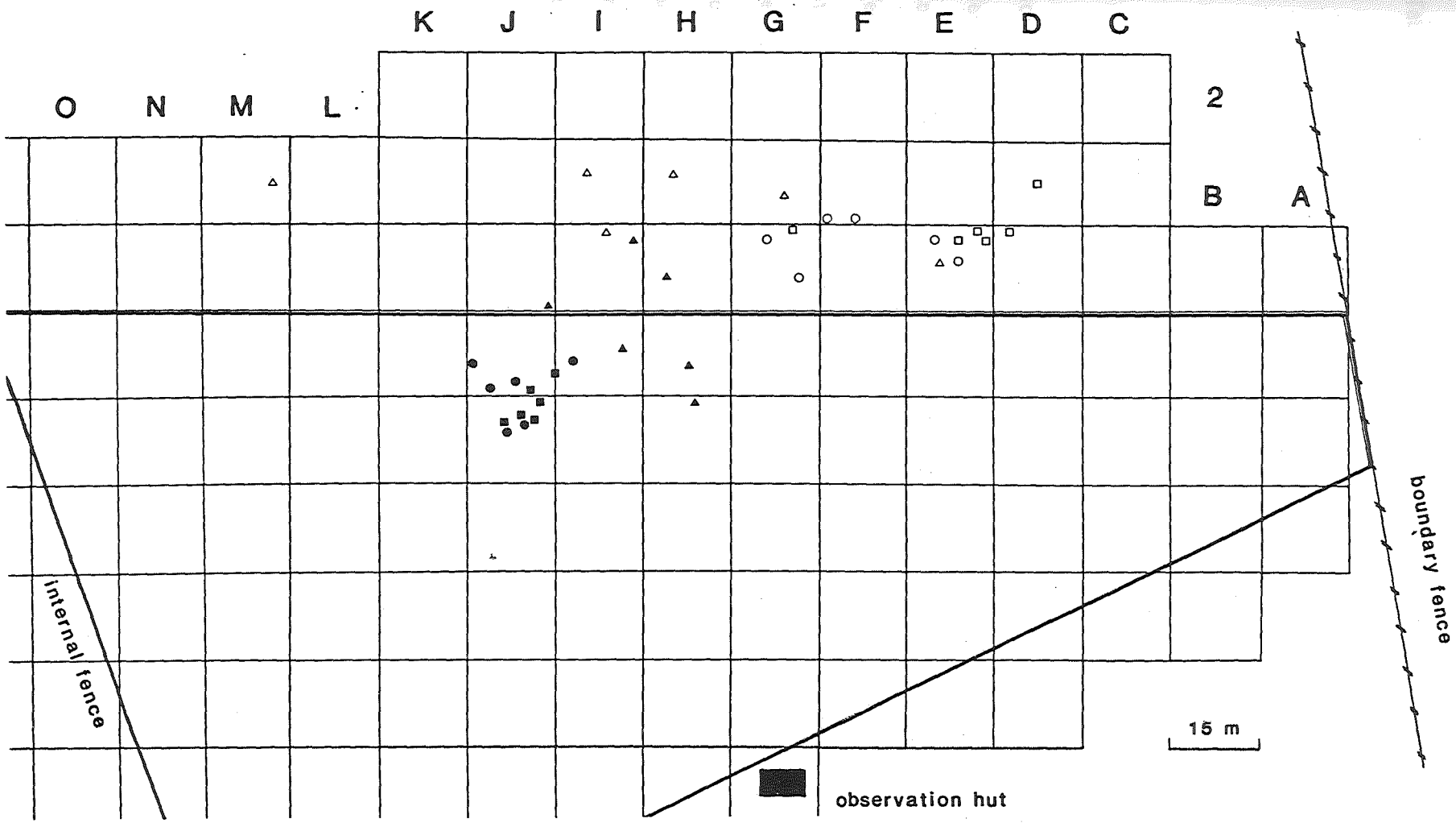


Figure 8.4 Centre of activity shifts between March and August 1982 for rabbits of different social status: M23(D) ▪, M46(I) •, M60(S) ▲, F42(D) ▫, F36(I) ○, and F84(S) △.

Table 8.9 Seasonal shifts of activity range (m) for male and female rabbits.

Sex	Season			
	Summer	Autumn	Winter	Spring
Males	7.7	17.6	12.4	25.0
Females	21.7	16.4	13.0	20.9

activity associated with the breeding season influenced movements. A marked decrease in activity range shifts for males followed in summer, possibly due to a more rigid social order among males (see section 7.2.1) compared with females. During summer the level of activity range shifts for females remained high. Breeding was still occurring during the summer months and metabolic requirements associated with pregnancy and lactation suggest that females have to maintain a high foraging rate. Female rabbits did spend more time feeding during spring and summer than males (see section 6.2.2), and as vegetation growth was not great during summer this could have caused some movement associated with the need to forage further.

All paired combinations of the factors sex, social status, and season produced significant variations in activity range shifts (see Table 8.7). The reasons for these differences are largely covered in the discussion above.

Age was another factor which influenced activity range shifts. As reported elsewhere (Myers and Poole 1961, Gibb et al. 1978, Daly 1979), shifts were more common among younger rabbits. At low densities Myers and Poole (1961) found that shifts occurred during the pre-breeding and breeding periods but at higher densities shifts occurred at all times of the year. Very few records were available for young rabbits (<9 months old) as it was difficult to establish age from observations alone, especially once juvenile rabbits acquired adult pelage (about 4–5 months old). Young rabbits of both sexes did shift their activity ranges more than adults, although for females this

Table 8.10 Shifts of activity range for adult and young rabbits of each sex, sample size in brackets.

Sex	Mean shift distance (m) Adults	Young
Males	13.3 (120)	21.9 (8)
Females	18.5 (114)	19.2 (9)

variation was small (Table 8.10). A more marked difference existed for males. This was expected since it is known that young females are more easily accepted into their parental social group than are young males (Mykytowycz 1959, 1960, Myers and Schneider 1964).

8.2.6 Dispersal movements

Although no special effort was made to examine dispersal movements, several instances of dispersal were noted. Four marked rabbits (M02, M14, M28, and F17) were found to have dispersed up to 1.5 km from the study area. Three of these rabbits were observed during spotlight counts of the Butchers Dam block by Rabbit Research Group (W D Ross pers. comm.) and a fourth was shot on an adjacent property. Only M02 was an adult when captured and marked in November 1980 (total wt.=1600 g). M02 was subsequently seen approximately 1.5 km from the study area during a spotlight count in the same month and again in July 1981. Also observed at the same point in July 1981 were M28 and F17. M28 was caught and marked in February 1981 as a juvenile (wt.=750 g) and was last seen on the study area in April 1981. F17 was one of the rabbits dug out in December 1980 (wt.=700 g) and was last observed in March 1981. Finally, M14 was shot approximately 500 m from the study area in May 1981. This rabbit had been captured and marked in January 1981 (wt.=1100 g) but never observed subsequently. Three of these rabbits (M28, F17, and M14) were all subadults when they dispersed. Juvenile animals with their sub-dominant status are

usually affected most by any type of social interaction resulting from increased population density (Christian and Davis 1964) and are therefore most likely to disperse. Other studies (Mykytowycz and Gambale 1965, Gibb et al. 1978, Henderson 1979) have also recorded the highest dispersal rates among juvenile and subordinate rabbits.

9 MARK-RECAPTURE

9.1 Introduction

Information from marked rabbits allowed analysis of behavioural aspects according to sex, age, and status. In addition, marked rabbits were essential to the poison experiment in the neophobia section of this study. Mark-recapture (MRC) techniques are also useful for estimating various population parameters, especially total numbers. Such analyses are based on a number of assumptions, of which equal catchability is the most crucial (Roff 1973b, Caughley 1977). This is rarely fulfilled with mammals, as numerous studies have shown (e.g. Getz 1961, Dunnet 1963, Kikkawa 1964, Tanton 1965). Daly (1980) has identified age, sex, and season as some of the factors affecting the trap response of rabbits and confirmed the unreliability of population estimates based on MRC techniques. Climatic factors have been related to capture success for gray squirrels **Sciurus carolinensis** (Perry et al. 1977) and eastern cottontails (Huber 1962).

Heterogeneity of trap response can also be caused by the particular trapping technique employed (Kikkawa 1964, Cormack 1966, 1968, Eberhardt 1969). Mammals are capable of modifying their behaviour in the light of experience, with the result that their behaviour is not stereotyped and innate but highly variable. Whereas many previous trapping studies of the rabbit have relied on the use of baited traps (Dunsmore 1974, Parer 1977, Daly 1980) the investigation of the neophobia hypothesis during the study precluded this approach. Instead, rabbits were caught during the course of their normal daily movements.

MRC data were used to investigate what factors influenced the rabbits' trap response and how accurately various population estimates calculated from the recaptures reflected the actual number of rabbits present on the study area. Sight counts obtained during the intensive behaviour observations each month were used for this comparison. Separate segments of the population were

examined to determine if the accuracy of population estimates could be improved. Efficiency of the trapping technique as indicated by the retention of tags and the amount of stress inflicted upon captured individuals was also examined.

9.2 Results

The population was live-trapped on 99 days from October 1980 to September 1982; trapping was carried out on 22 of the 25 monthly field trips. A total of 183 rabbits were caught and individually marked. The majority of these (85%) were caught using smeuse traps while the remainder (15%) were dug out. Many of these marked rabbits (35%) were subsequently recaptured. Only a proportion of the total population ventured inside the fenced area so not all rabbits in the observed area were available for marking. A comparison of the number of marked rabbits seen each month with the estimated population size (Figure 9.1), as indicated by mean daily maxima from sight counts, suggests that approximately 40-50% of the population were marked. Towards the end of the study this proportion increased to about 60% of the population.

MRC data were examined for differences in trap response related to season, and to the sex and age of the rabbit. Although the trapping regime varied widely from month to month, mainly in an attempt to overcome the rabbits' 'awareness' of set traps (see section 9.3), valid comparisons can be made by calculating the results on a catch per unit effort basis. Initially, a number of the traps remained set on most days of each monthly trip but, due to decreases in capture rates and the creation of a 'fence-effect', the number of days on which traps were set was reduced after the first seven months of the study to either 1, 2, or 3 days. The fence-effect became obvious after several months of trapping; many rabbits changed their daily movement patterns and concentrated their feeding activities on the northern and eastern parts of the study site, outside the fenced area. The number of rabbits caught was not significantly correlated with the number of trap events ($r=0.40$, NS) (Figure

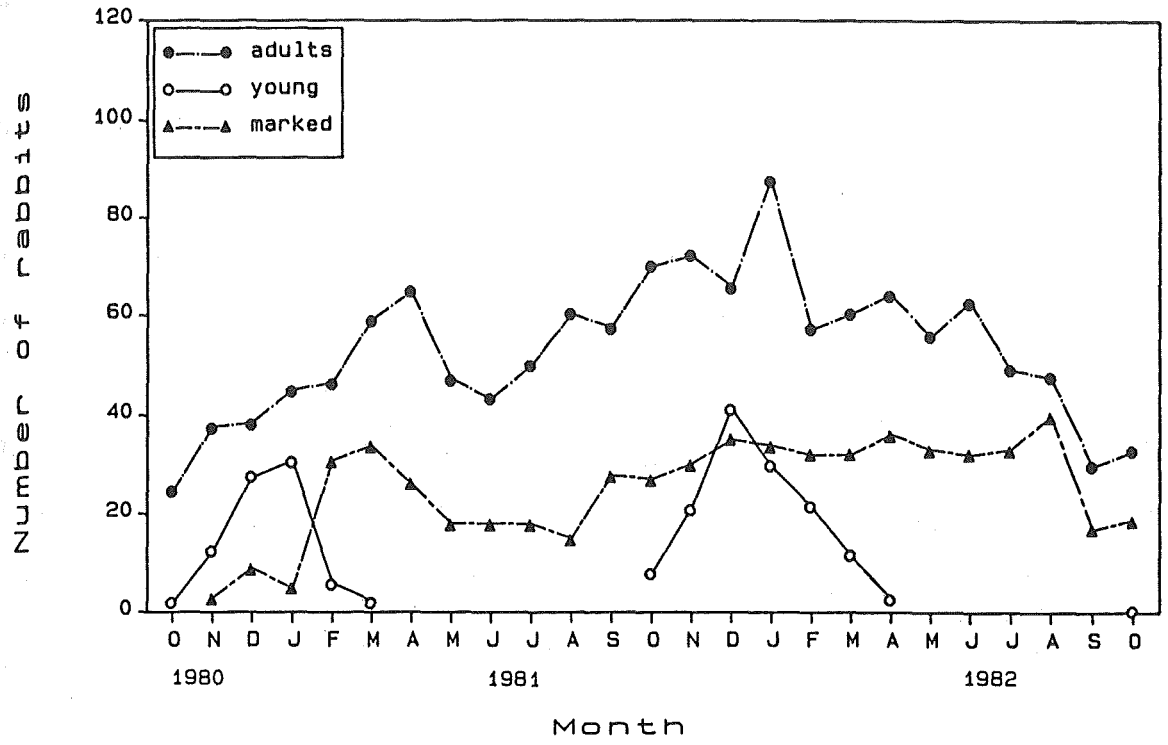


Figure 9.1 Comparison of the estimated number of adult and young rabbits present with the number of marked rabbits observed each month.

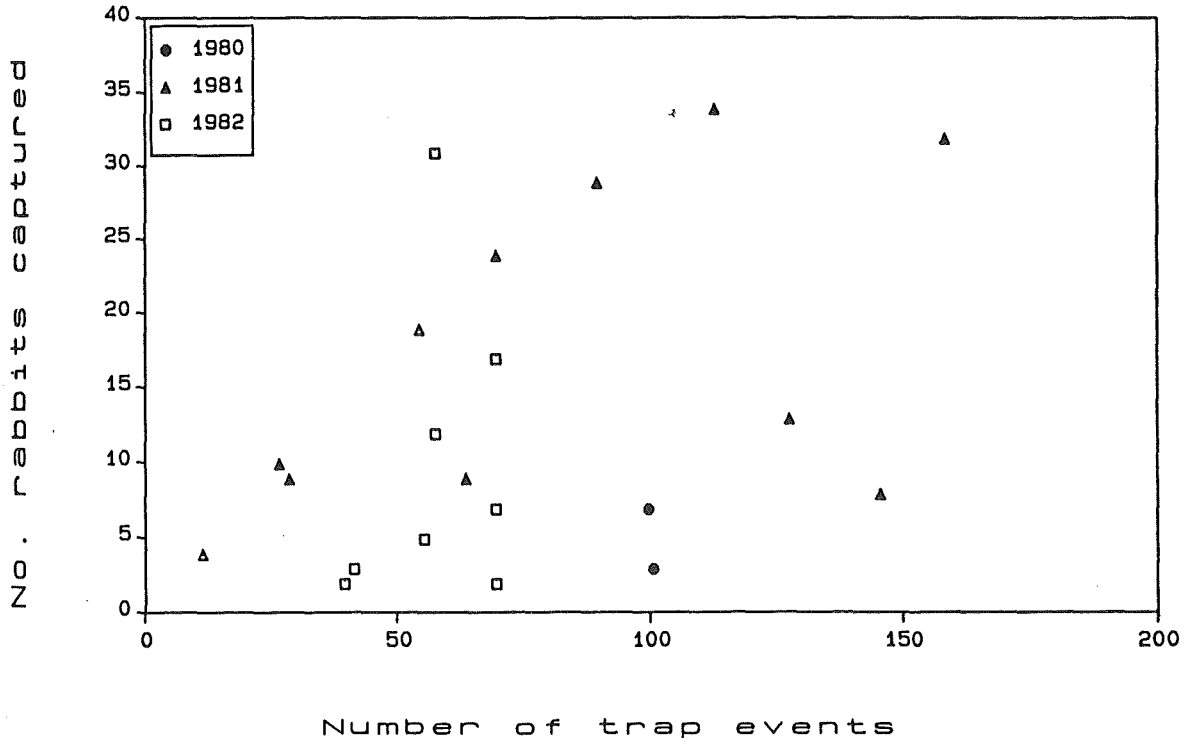


Figure 9.2 Comparison of the number of trap events with the number of captures each month.

9.2). In this case a trap event is defined as one trap set for 24 hours.

9.2.1 Seasonal variation

Adult rabbits are sedentary, rarely changing their basic movement patterns (Southern 1940, Mykytowycz and Gambale 1965, Parer 1982), so variation in the number caught each month reflects variation in the population size and individual trap response. Monthly trapping results were adjusted for the number of trapping events to give a catch per unit effort result (Figure 9.3). Trapping success was highest in spring and summer and lowest during autumn and winter. This variation was related to the number of rabbits present with the greatest number of captures occurring when population levels were highest. The close correlation between trapping success and population levels ($r=0.73, p<.001$) is also due to the inclusion of young rabbits in the results and their greater trappability (see section 9.2.3).

Nevertheless, when trapping success is adjusted for population size (based on the mean daily maxima from sight counts) and young rabbits are excluded from the analysis, the capture success for adult rabbits was still significantly higher during the spring and summer months (Duncan's new multiple range test, $p<.05$) (Figure 9.4). Periods of greater trappability coincide with increases in the number of rabbits moving into the fenced area, and the occurrence of breeding in the population. These features are associated with the main growth phase for vegetation, and the area within the fence line has the greatest concentration of palatable species.

9.2.2 Sexual variation

The number of male and female rabbits captured each month is shown in Table 9.1 together with the probability that the observed deviation in the sex ratio was due to chance alone. Comparisons were made using the sex ratio of the marked rabbits seen each month. The proportion of females in the population was 0.51 in both years (34/67 from October 1980 to September 1981,

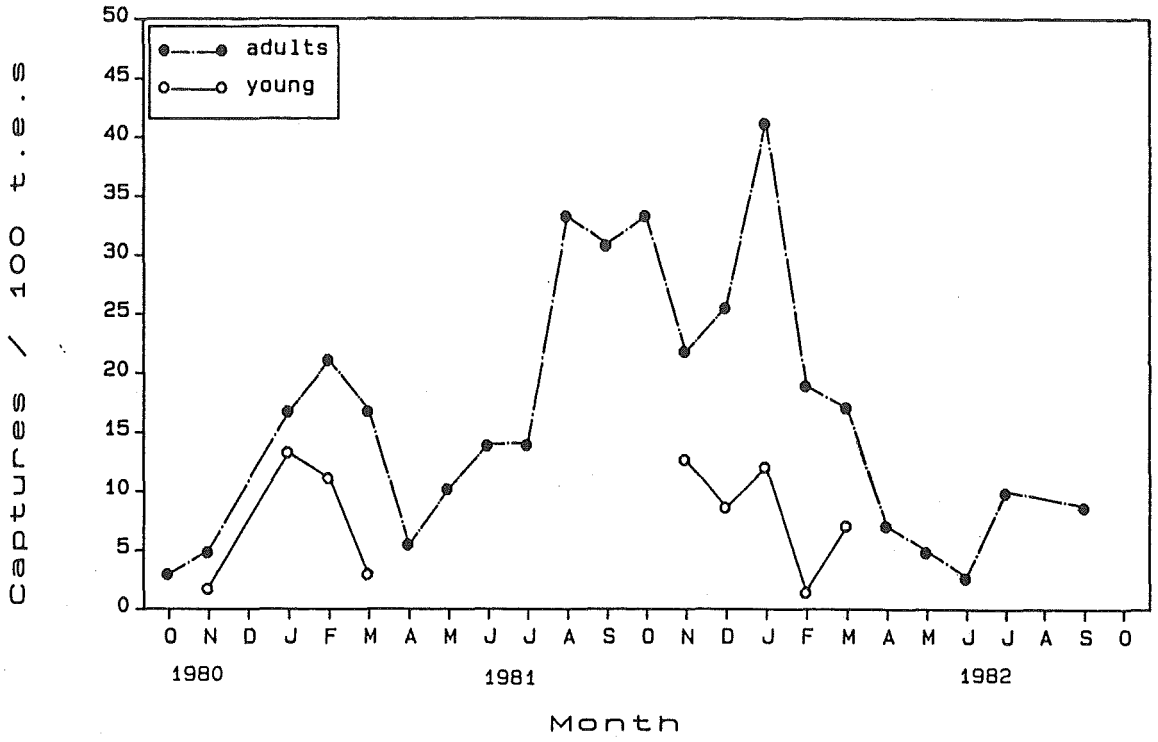


Figure 9.3 Monthly catch per unit effort indicated by the number of captures per 100 trap events.

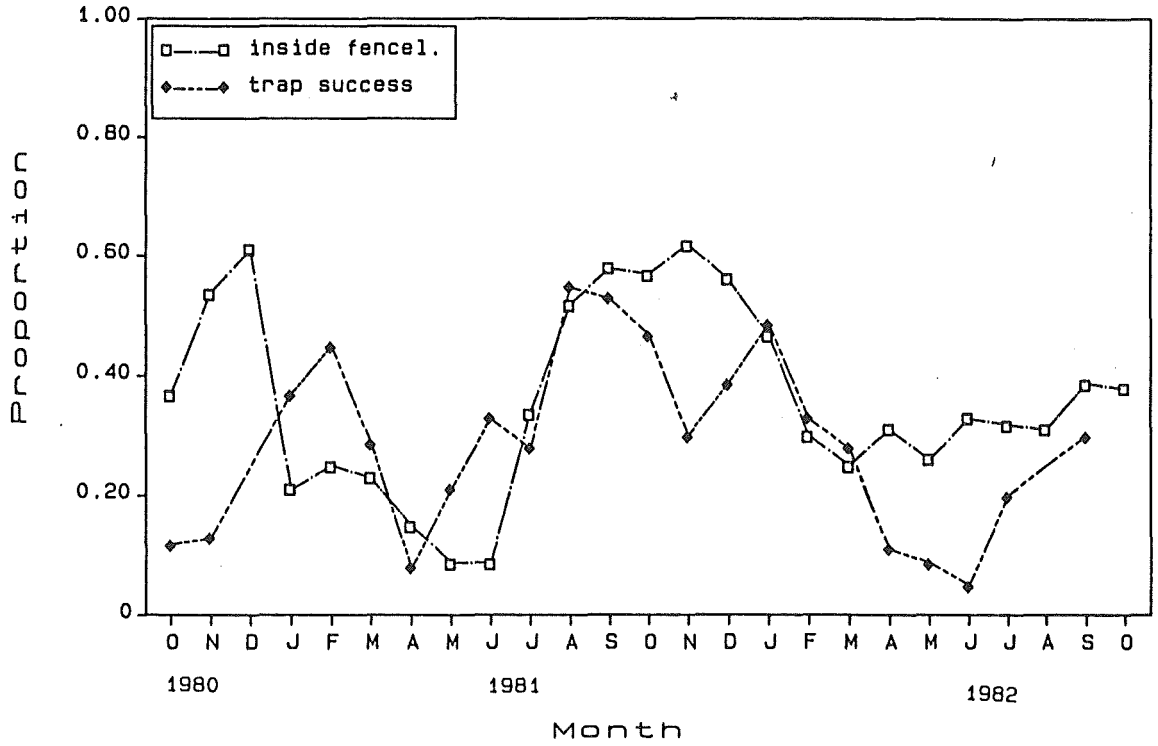


Figure 9.4 Comparison of trapping success (captures per trap event) for adult rabbits, adjusted for population size, with the proportion of the population observed inside the fence line each month.

Table 9.1 Number of male and female rabbits trapped each month; test used is either chi-square contingency test (C) or Fisher exact probability test (F).

Month	Males	Females	Test	Exact probability (x100)	
Oct 1980	1	2			
Nov	1	6	F	8	
Dec	–	–			
Jan 1981	15	19	C	53	
Feb	7	22	C	1.3	*
Mar	14	18	C	68	
Apr	4	4			
May	3	10	C	22	
Jun	4	5			
Jul	5	4	F	68	
Aug	4	0			
Sep	3	6	F	58	
Oct	5	5	F	75	
Nov	7	12	F	22	
Dec	7	17	C	8	
Jan 1982	12	19	C	33	
Feb	10	2	F	3.1	*
Mar	4	13	F	3.7	*
Apr	1	2			
May	1	1			
Jun	0	2			
Jul	3	4			
Aug	–	–			
Sep	2	3	F	24	
Oct	–	–			

* $p<.05$

44/87 from October 1981 to October 1982). Depending upon sample size, either a chi-square contingency test ($n>20$) or a Fisher exact probability test was used. Consecutive monthly data sets with small sample size were combined.

Although the difference in the proportions of each sex trapped is only significant in three samples, the overall trend is towards a greater number of females trapped throughout the year (females predominate in 16 out of 22 months, cf. males in 3 out of 22 months). The significant difference in favour of males in February 1982 is anomalous and could possibly be a Type I error related to the small sample size. The trend in favour of females is especially

Table 9.2 Distribution by sex of trapped rabbits.

	Males	Females	Total
Initial captures	74	81	155
Recaptures	37	95	132
Total	111	176	287

clear when the data are smoothed to eliminate biases caused by months with a low number of captures (Figure 9.5).

When all data are pooled (Table 9.2) it is evident that, although male and female rabbits did not differ significantly in the number of initial captures (chi-square=0.32,NS), recaptures were significantly in favour of females (chi-square=25.49,p<.001).

The total number of times an individual was captured (Table 9.3) was compared for males and females using a chi-square contingency test. The distributions are significantly different (chi-square=8.07,df=3,p<.05), with females having a higher probability of capture (.1263) compared with males (.0795).

Table 9.3 Distribution of total number of captures for male and female rabbits.

	Number of captures				
Sex	1	2	3	4 or more	Total
Males	53	12	6	3	74
Females	48	13	5	15	81

The greater trappability of females is also evident if those individuals which were captured 3 or more times are examined. Among females this comprised 25% (20/81) of the population compared with only 12% (9/74) for males. The

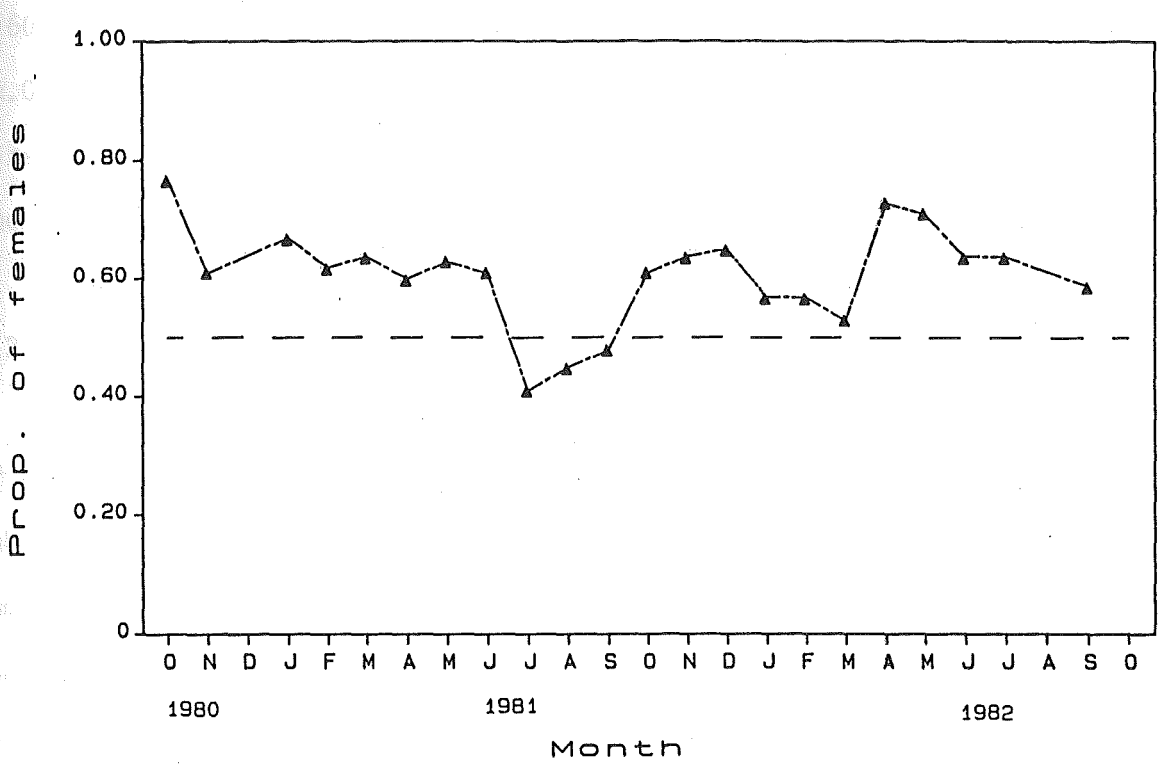


Figure 9.5 Proportion of female rabbits captured each month; data were smoothed according to the formula b = (a+b+c)/3.

incidence of more than one recapture in the same trap also reflects this feature. Twelve individuals were caught in the same trap more than once and in every case they were female rabbits. The proportion of recaptures in the same trap was compared for males (0 recaptures in the same trap/34 recaptures in total) and females (12/103) and tested for independence (Sokal and Rohlf 1969, p.609). The result was highly significant in favour of females ($t=3.52$, $p<.001$). However, as the reliability of this test is dependent on the sample size there is only an 80% certainty of having detected a 'true' difference at the 5% level of significance in this example.

9.2.3 Trappability of young

Young rabbits are more easily caught than adult rabbits at certain times of the year. After relatively low levels initially, the capture rate for young rabbits increases markedly towards late summer and early autumn. Although the number of young captured is correlated with the number of young observed in the population ($r=0.62, p<.05$) (Figure 9.6), the dominant factor determining the trappability of young is probably size or size-related behaviour. Many young rabbits were observed in the vicinity of the smeuse traps; on most occasions they appeared nervous and often fled if wind caused the doors to move. Frequently, numerous inspections would be made before a young rabbit ventured into a trap. Also, young rabbits were commonly seen moving freely through the netting of the fence.

When young rabbits reached a weight of approximately 750 g they became markedly more catchable (Figure 9.7). Despite the obvious presence of young rabbits, only seven individuals less than 750 g were caught (cf. 51 rabbits between 750 and 1050 g). The numbers of young male and female rabbits trapped were compared with sex ratio of the adult population. Although the difference is not significant for initial captures (chi-square=2.27, NS), it is significant when recaptures are included (chi-square=5.39, $p<.05$), with young females being captured more frequently than young male rabbits.

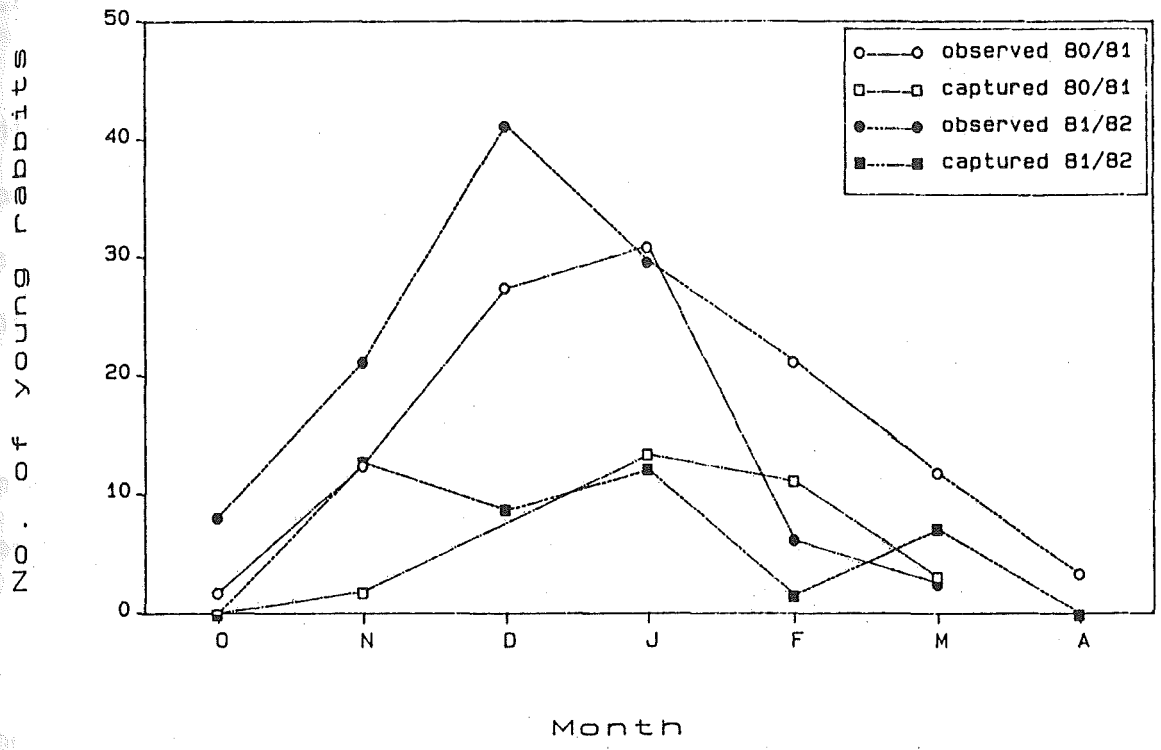


Figure 9.6 Number of young rabbits observed and captured for the periods October 1980–April 1981 and October 1981–April 1982.

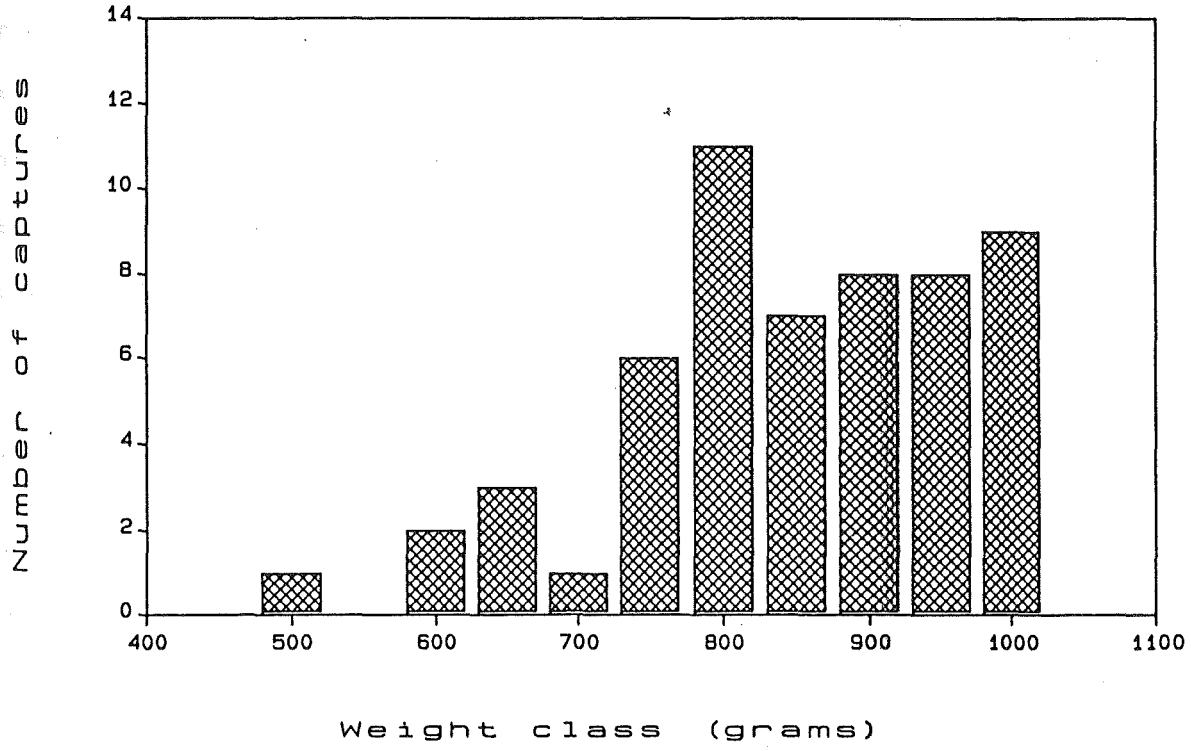


Figure 9.7 Distribution of captures by weight class for rabbits up to 1000 g.

9.2.4 Individual variation in trap response

The recapture data for adult rabbits were examined for individual differences in trap response over an 11-month period. If all rabbits had the same probability of being caught (p), then the number of times an individual is recaptured (x) over a given number of trapping occasions (n) is binomially distributed (Geis 1955):

$$p(X=x) = \binom{n}{x} p^x (1-p)^{n-x} \qquad (1)$$

An estimate of the probability of capture can be calculated from the observed recapture data using:

$$p = \frac{fx}{n(N+N_o)} \qquad (2)$$

where fx is the total number of trap events, N is the total number of different rabbits caught and N_o is the total number not caught. This technique was first used by Orians and Leslie (1958) in their study of shearwaters **Procellaria puffinus**. Only previously marked rabbits were used for this analysis so that N_o was known. Other workers have calculated N_o from the estimated total population size over the sample time but the data in this analysis have been derived from different 12-month periods. Hence, the initial capture has been ignored and the analysis is for an 11-month trapping period. The binomial probability of capture was calculated from equation (2) as follows:

$$p = \frac{39}{11(19+15)}$$

$$= 0.1043$$

The expected distribution of recaptures was calculated using equation (1) and compared with the actual distribution (Table 9.4) using a goodness-of-fit chi-square test.

The observed recapture distribution is significantly different from the binomial distribution (chi-square=9.67, df=3, $p<.05$). The discrepancy

Table 9.4 Observed and expected recapture frequencies of rabbits over an 11-month period.

	Number of recaptures						
	0	1	2	3	4	5 or more	Total
Observed	15	8	4	5	2	0	34
Expected	10	13	8	3	1	0	35

between the observed and expected totals is due to rounding error. Deviation from random trapping could have been due to a number of reasons:

1 male and female rabbits may differ in their trappability,

2 seasonal effects may have influenced the results, and

3 individual rabbits may not have a constant probability of being trapped.

Each of these possibilities is examined below.

1 Sex differences

As previously shown (see section 9.2.2), male and female rabbits do differ in their relative trappabilities. The recapture distributions for each sex over the 11-month period were compared (Table 9.5) using a chi-square contingency test. Although the distributions are not significantly different (chi-square=5.27, df=4, $p>.20$), the probability of capture for females (0.1263) is higher than that for males (0.0795). These two probabilities were used to generate expected recapture distributions for male and female rabbits separately. Although the distribution for males showed no deviation from random trapping (chi-square=0.33, df=3, $p>.95$), females were not randomly captured (chi-square=11.53, df=4, $p<.05$). The probability of capture for males is quite low and near the level at which Ricker (1937) recommends that the Poisson distribution should be used. Hence male rabbits may not be randomly caught, but with this method of analysis and the small sample size any possible deviation from randomness cannot be detected. Larger data sets were

Table 9.5 Recapture frequencies for male and female rabbits over an 11-month period.

Sex	Number of recaptures 0	1	2	3	4 or more	Total
Males	7	5	3	1	0	16
Females	8	3	1	4	2	18

available for 9- and 7-month periods and, although neither gave significant results, the level of probability decreased noticeably as the recapture sample size increased (9-month period, $p>.50$; 7-month period, $p>.30$).

2 Seasonal effects

As the data used in this analysis came from 12-month periods (including the month of initial capture) each individual's data set covered a full year. There was no bias towards any season for the month of initial capture among the individuals examined, so seasonal variation (as shown in section 9.2.1) cannot be responsible for the non-random trapping.

3 Constant probability of capture

Too few individuals had data sets covering more than 12 months which would have permitted further checks on relative recapture rates, based on previous trap experience recorded in the initial 12 months. Instead, rabbits were classified as 'low' trappability individuals (0, 1, or 2 recaptures for the 11-month period) or 'high' trappability individuals (3 or more recaptures). These two groups were compared with respect to the number of individuals caught more than once in a particular month, using the Fisher exact probability test (Table 9.6). The difference between the within month recapture rates for these two classes of individuals is highly significant ($p<.001$). Low trappability or trap-shy rabbits were frequently observed. They would approach a trap, inspect it briefly and then jump away as if alarmed.

Table 9.6 Within-month recaptures for rabbits with 'low' and 'high' trappability.

	Recaptured	Not recaptured
'Low' trappability	1	24
'High' trappability	6	3

Thus non-random trapping appears to result from unequal probabilities of capture for males and females as well as unequal trappability of individuals. Incorrect estimation of the N_o class has caused problems in other studies (Tanton 1965, Edwards and Eberhardt 1967, Daly 1980) but in this case data were selected so that N_o was known and could not have decreased the accuracy of the probability of capture calculation.

9.2.5 Population estimates

Although it has already been shown that catchability was not constant, an important assumption for most population estimation techniques, various methods of population estimation have been tested to determine which gives the best results within the limitations. The results presented support Caughley's (1977) criticism of workers who demonstrate a lack of equal catchability, or the fact that the population is not closed, but then ignore these violations and proceed to use population estimators in an erroneous way.

Two forms of population estimation have been examined: monthly estimates, and estimates of the mean population size for the total duration of the study. The month to month methods used were:

1 the Schnabel method,

2 the Schumacher-Eschmeyer method,

3 Marten's regression method, and

4 the Jolly-Seber model.

Table 9.7 Various monthly population estimates based on MRC data and resightings, compared with sight counts.

Month	Schnabel	Schumacher -Eschmeyer	Marten's regression	J-S MRC	J-S MRC&Res	Sight counts
Oct 80	–	–	–	–	–	24
Nov	38	20	6	124	20	48
Dec	–	612	–	135	37	64
Jan 81	95	121	118	74	90	73
Feb	96	119	46	67	54	52
Mar	78	88	37	76	53	60
Apr	76	89	44	44	44	65
May	73	83	40	32	37	48
Jun	67	73	–	97	32	43
Jul	67	72	37	88	34	50
Aug	70	76	44	66	45	61
Sep	72	78	41	142	43	58
Oct	70	76	41	132	41	76
Nov	74	79	52	1439	54	90
Dec	77	83	57	120	57	104
Jan 82	91	102	92	–	103	113
Feb	93	105	61	–	65	78
Mar	92	102	59	–	62	69
Apr	93	103	59	–	55	67
May	93	103	46	–	48	59
Jun	93	–	44	–	48	59
Jul	91	100	42	–	46	49
Aug	–	–	–	–	48	48
Sep	93	99	23	–	24	30
Oct	–	–	–	–	–	34

The Jolly-Seber model was used on two forms of data, firstly recaptures only and then recaptures and resightings. Marten's (1970) regression method also employs a non-capture sampling component in its calculation. The Schnabel and Schumacher-Eschmeyer methods assume a closed population (no births or immigration, no deaths or emigration), equal catchability, and no tag loss (Davis and Winstead 1980). Marten's regression method relaxes the restriction of equal catchability, while the Jolly-Seber model assumes equal catchability but allows for loss of individuals (death and emigration) and dilution (births and immigration) (Jolly 1965, Seber 1965). Results from these analyses are compared with the estimates from sight counts, calculated as the mean of the daily maxima seen during transect sampling (Table 9.7, Figure 9.8).

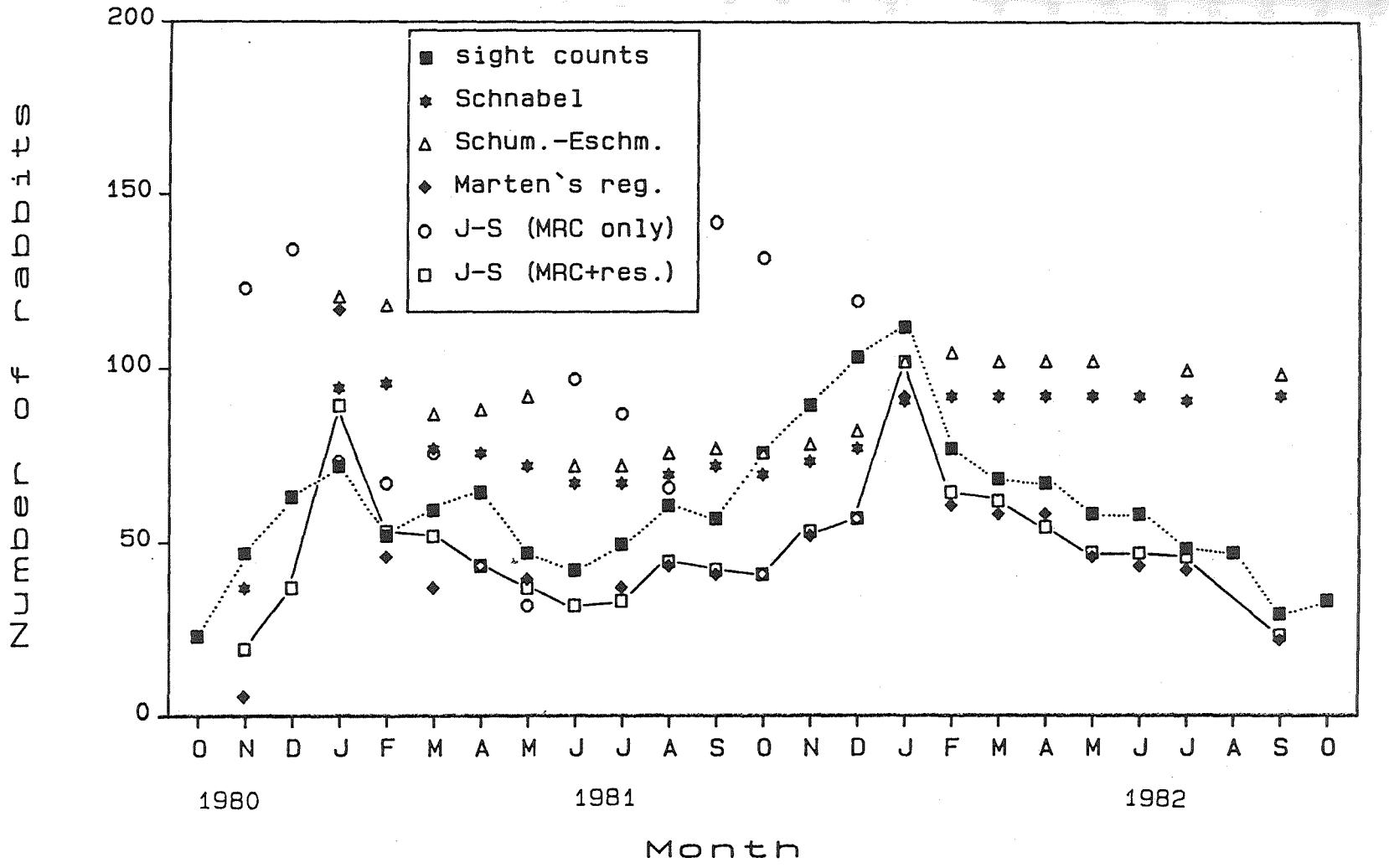


Figure 9.8 Comparison of population estimates calculated from MRC data with an estimate of population size from sight counts.

The second set of analyses involved population estimates of the mean size of the population for the total duration of the study. Frequency of capture data was applied to a number of models each based on different zero-truncated frequency distributions. The data were fitted to zero-truncated Poisson, negative binomial, and geometric distributions and the shape of the distribution was used to estimate the missing zero-class (i.e. the unknown number of rabbits that were never caught). Population size can then be calculated as the number of rabbits captured at least once plus the estimated number that were never caught. The data used in this analysis complied with the assumption of a closed population.

Each of the three distributions are based on different assumptions about the catchability of individuals, although they do not cover the complete range of possibilities (Caughley 1977). The Poisson and negative binomial methods rely on the calculation of the mean capture frequency from the observed data while the geometric estimate relies on the parameter q, the probability that a given individual will be captured at least once. The Poisson distribution (a limiting case of the binomial distribution) is characterised by the assumption that random captures occur whereas the negative binomial and geometric distributions reflect varying degrees of unequal catchability. The negative binomial is often indicative of a population in which both trap-prone and trap-shy individuals are present (Caughley 1977). The recapture data for the 12-month periods were applied to these models (Table 9.8) and the generated frequencies (E[fi]) were compared with the observed recapture frequencies (fi) using a chi-square goodness-of-fit test as shown below:

$$\text{chi-square} = \frac{(fi-E[fi])^2}{E[fi]}$$

for each i down to i=3, the frequencies being pooled for all subsequent classes.

Table 9.8 Zero-truncated Poisson, negative binomial and geometric distributions fitted to recapture frequencies of rabbits over a 12-month period.

Number of captures i	Number of individuals fi		Poisson E[fi]	Negative binomial E[fi]	Geometric E[fi]
1	15		12.224	37.707	15.583
2	8		10.922	28.083	8.441
3	4		6.506	16.951	4.572
4	5		2.907	9.036	2.477
5	2		1.039	4.435	1.341
6	0		0.309	2.052	0.727
7	0		0.079	0.908	0.394
8	0		0.018	0.388	0.213
9	0		0.004	0.161	0.115
10	0		0.001	0.066	0.063
11	0		0.000	0.026	0.034
12	0		0.000	0.010	0.018
		chi-square	3.981	43.881	0.603
		df	2	1	2
		p	>0.10	<0.001	>0.70
		Estimated N	41	48	63

The closest fit to the observed data was given by the geometric distribution ($p>.70$) and, not unexpectedly, the negative binomial gave the worst ($p<.001$). In this situation where there was no enticement (e.g. baits) to enter the traps, individuals would not be expected to exhibit trap-proneness. Instead most variation would occur in the degree to which individuals became trap-shy. The population estimate from the geometric model (63) was extremely close to the mean of the monthly sight counts (64) when the two post-poisoning months were omitted. When the male and female segments of the population were examined separately the geometric distribution once again gave the best estimates.

Edwards and Eberhardt (1967) modified the geometric distribution function to apply only to the capture frequencies ($x=1,2,...n$). They manipulated the maximum likelihood estimation (MLE) for the geometric distribution to give:

$$N = \frac{nx}{1 - (nx/x.nx)}$$

where x.nx = the total number of captures,

nx = total number of individuals captured, and

N = the estimate of the population size.

Therefore, using the capture data for the 12-month period,

$$N = \frac{34}{1-(34/73)}$$

$$= 63.6$$

which is very close to the other geometrically derived estimate.

9.2.6 Tag loss

The accuracy of calculations from MRC data partly depend upon the permanence of the marking system. Therefore it was important to check if tag loss had occurred among those individuals that were marked. Two types of data were available: firstly, monthly MRC data and, secondly, the sample of rabbits killed during the poison experiment in August 1982.

Of the 132 recaptures during the study, 9 were of rabbits that had previously been marked but had lost their colour-coded tag. Except for a few rabbits marked very early in the study before Monel tags were available, their identity could be deduced from the numbered Monel tag they also carried. In these cases the only sign that they had been marked previously was a rip in the lower ear where the tag had pulled out. Tag loss was calculated as follows:

$$\text{tag loss} = \frac{\text{no. recaptured with tag missing}}{\text{total no. of recaptures}} \times 100$$

$$= 9/132 \times 100$$

$$= 7.3\%$$

For the non-capture sample obtained during the poisoning of the population another estimate for tag loss could be calculated as:

$$\text{tag loss} = \frac{\text{no. killed with tag missing}}{\text{total no. of tagged rabbits killed}} \times 100$$

$$= 1/16 \times 100$$

$$= 6.3\%$$

By determining the mean length of time that each rabbit had been present, this figure can be adjusted to give an annual tag loss estimate. For those individuals killed during the poison experiment the mean length of time present was 10.4 months, or 0.87 of a year. Hence,

$$\text{annual tag loss} = \frac{6.3}{0.87}$$

$$= 7.2\%$$

9.2.7 Disappearance rates and stress

Another assumption for MRC methods of estimating population parameters is that marked individuals are not affected (either in behaviour or life expectancy) by being marked (Southwood 1966). The use of two different capture techniques provided the opportunity to test for variation in the amount of stress caused by these methods of capture. Additionally, among the rabbits that were captured by digging out a number were transported to the site from outside the area, in some cases a distance of over 2 km. The disappearance rates associated with each method are shown in Table 9.9. For consistency only rabbits caught in smeuse traps in those months when digging out occurred are included.

The disappearance rates may have been influenced by the age distribution of the rabbits captured. In the samples dug out there were many more young rabbits than adults (Table 9.10). The effect of greater stress is evident where rabbits have been transported to the area after being dug out at other locations, as they have the highest disappearance rate (50%).

Table 9.9 Disappearance rates of rabbits caught in smeuse traps and by digging out.

Capture method	n	Disappearance rate (%) Males	Females	Total
Smeuse trap	15	16.7	11.1	13.3
Dug out (within area)	20	28.6	30.8	30.0
Dug out (outside area)	8	50.0	50.0	50.0

n = number of rabbits

Table 9.10 Weight (age) distribution of rabbits captured by digging out.

Weight class (g)	Males	Females	Total
0 - 1000	10	14	24
> 1000	1	3	4
Total	11	17	28

Over the duration of the study the disappearance rate for marked rabbits corresponded roughly with the number of hawk sightings made each month (Figure 9.9). Predation by hawks was very evident, especially during the spring and summer months when large numbers of young rabbits were present. Not enough sightings were made of ferrets and feral cats to determine their relationship with the disappearance rate.

9.3 Discussion

A number of factors appeared to influence a rabbit's chance of being trapped, notably season, and the age and sex of the individual. Also, there was considerable individual variation in trap response within the population.

Trapping success was highest in the spring and summer months, although the inclusion of young rabbits in the results exaggerated this trend. The

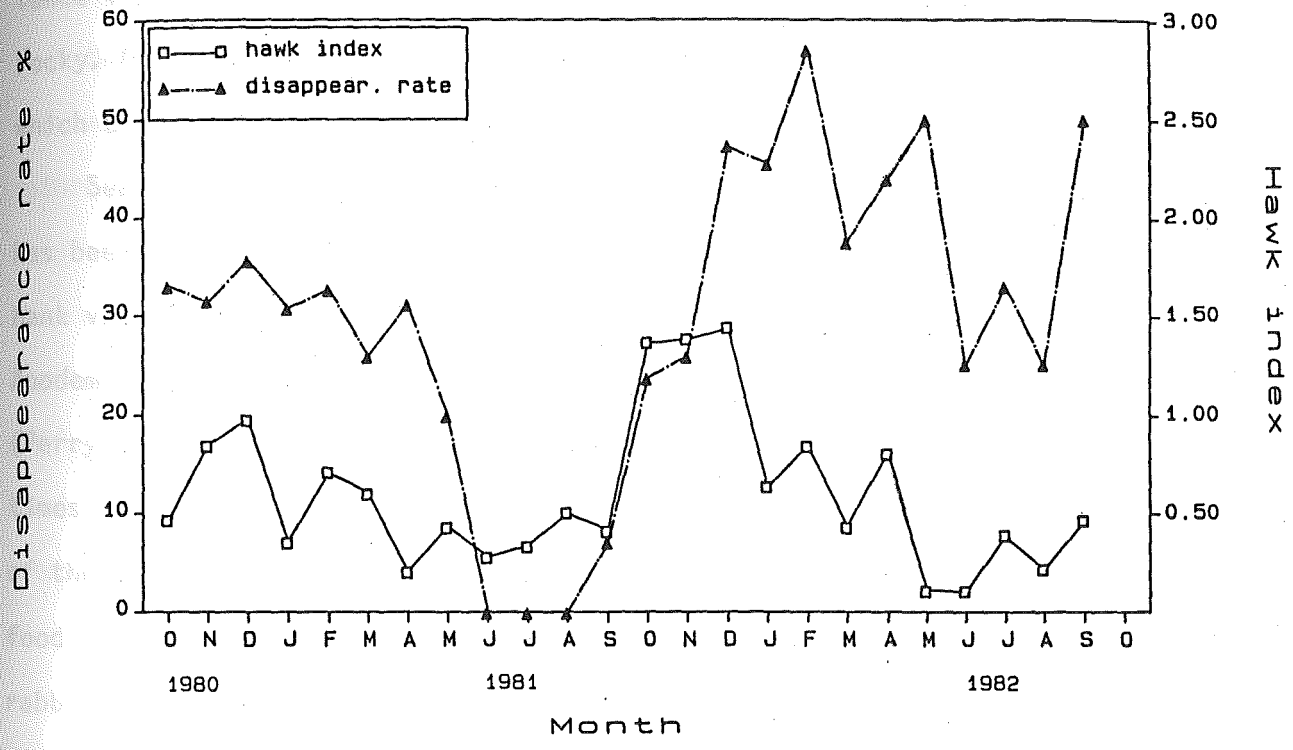


Figure 9.9 Disappearance rate of marked rabbits compared with an index of the number of hawk sightings each month.

increased trappability of adult rabbits during this period was associated with a higher proportion of the population frequenting the fenced area. This influx coincided with the increased occurrence and the growth period of many preferred vegetation species inside the fence line, and also the incidence of breeding in the population. Digging of breeding stops was possible within the fence line in contrast to much of the remainder of the area which was too rocky. Also, several females used abandoned burrows inside the fence line in which to drop their litters.

Seasonal variation in trap response is not uncommon in small mammals. It has been recorded for the cottontail rabbit (Huber 1962, Bailey 1969), the bank vole **Clethrionomys glareolus** (Kikkawa 1964, Tanton 1969), the woodmouse **Apodemus sylvaticus** (Kikkawa 1964, Tanton 1965), and the gray squirrel (Perry et al. 1977). In most cases the increase in trappability at certain times of the year is associated with increased movement and often an extension of the animal's range in response to changing environmental features, notably food supply. Huber (1962) found a decrease in trapping success for cottontail rabbits with snow or heavy rain and associated the decrease with reduced movement. Parer (1977) and Daly (1980) have also recorded seasonal variation in trap response for the rabbit in Australia. In both studies enhanced trapping success coincided with periods of food shortage; rabbits entered traps primarily for the bait. This is analogous to the changes in movement caused by habitat effects which were evident in this study.

Adult rabbits were not randomly trapped; this was the result of unequal probabilities of capture for males and females, as well as unequal trappability of individuals. Heterogeneity in trap response has also been observed for woodmouse and bank vole populations (Kikkawa 1964, Tanton 1969), as well as for cottontail rabbits (Geis 1955, Huber 1962, Eberhardt et al. 1963, Bailey 1969).

Sexual variation in trap response was caused by the greater frequency of recaptures among female rabbits. Although there was a similar ratio for

initial captures, females outnumbered males by almost 3:1 for recaptures, a trend also found for cottontail rabbits (Chapman and Trethewey 1972). Parer (1977) and Daly (1980) found sexual variation in trap response, but only during the pre-breeding season. Unfortunately their results are contrary to each other, indicating that more than one factor is responsible for the observed variation in trappability.

Male and female rabbits were reasonably similar in their emergence times and early movement patterns (see section 5.2), therefore discounting any trap saturation effect by one sex. In fact, capture rates were so low that trap saturation was never a problem. A number of females were caught in the same trap more than once whereas same trap recaptures never occurred for males. The higher probability of capture for females could indicate an inherent difference in response to traps related to different physiological status. Food supply is more critical for females, especially with increased energy requirements during the breeding season, and may lead to higher motivation to enter the fenced area where vegetation growth was greatest.

In addition to differences between the sexes, individual variation in trap response occurred with some rabbits showing low trappability and others high trappability. Heterogeneity of the habitat undoubtedly played a role. An individual rabbit's propensity to be captured was partly dependent on the proportion of its range included within the fenced area. Some individuals may have had an inherently stronger exploratory drive which caused them to enter the traps more frequently. Also, experience with the traps may have altered particular individual's responses. After confinement and handling some rabbits would become more cautious and less likely to enter traps on subsequent occasions.

Despite their more frequent movement into and out of the fenced area, adult rabbits remained more difficult to catch than younger individuals, perhaps indicating an increased caution with age. Mykytowycz and Gambale (1965) found that adult rabbits could be alerted by the setting of trap doors

and were less likely to enter the trapped area.

The trappability of young rabbits increased markedly from low levels early in the breeding season to a peak during late summer and early autumn. Very young rabbits seldom move far from the breeding stops. When they do begin to range further they are still small enough to get through the netting of the fence and traps, although many of those observed appeared very reluctant to venture near the traps. The trappability of young rabbits was directly related to their size, with a distinct rise in the numbers caught at a weight of 750 g. This size level may indicate a point above which young rabbits can no longer move freely through the netting. The considerable number of young weighing between 750 and 950 g which were found with their heads caught through the netting of the traps supports this view. This weight level may also mark an increase in the degree of use of the smeuse traps by young rabbits, and correspond to the period when juveniles are becoming more exploratory and are beginning to disperse. Daly (1980) found that trappability increased with age in young rabbits and declined at sexual maturity, a pattern also recorded for the cottontail rabbit (Huber 1962, Bailey 1969).

Results from estimates of monthly population numbers by different methods suggest that MRC data should be used with caution to estimate population size, especially when the basic assumptions of the methods are not satisfied. Sight counts have been used frequently in population censuses (e.g. Talbot and Stewart 1964, Douglas 1967, Caughley et al. 1984). Myers (1954, 1957) and Dunnet (1957c) used sight counts for estimating the number of rabbits in an area. Myers (1957) concluded that there was an inverse relationship between the accuracy of the sight counts on one hand, and the warren size and the presence of young on the other. Both these workers considered that reasonably accurate estimates of population size could be gained from sight counts, as long as patterns of emergence and disturbance features (such as predators or human interference) are taken into account. In this study the sight counts were calculated as the mean of the daily maxima from each days observations.

Therefore the counts are serially independent and calculation of the variance is possible.

The Schnabel method tends to smooth the data by accumulation, and therefore estimates of population size over a period of time are deceptively uniform. Davis and Winstead (1980) experienced this problem when applying the technique to cottontail rabbits. The Schumacher-Eschmeyer method also responds very slowly to population changes because of its accumulative nature. This method resulted in gross inaccuracies for the first few months when samples were small. Marten's regression method consistently underestimates the population size although it responds well to changes in total population size.

Currently the Jolly-Seber stochastic model is the most efficient method for estimating population statistics in studies where the recapture histories of individuals are known (Southwood 1966, Wilbur and Landwehr 1974). Of the two forms of Jolly-Seber analysis used, that based on resightings as well as recaptures was far superior. The low number of captures in the second year of the study and hence few recaptures of previously marked rabbits meant that no estimates were available from January 1982 onwards based on MRC data only. The closest correlation with the actual population size given by sight counts was attained using the Jolly-Seber model on recapture and resighting data. To some extent the inclusion of resighting data overcame the reliance on numbers actually captured each month. This method tended to slightly underestimate the population size, but closely parallel relative increases and decreases in the population from month to month. Some underestimation was expected, however, as not all rabbits in the population came into contact with the traps. Some individuals had their entire ranges outside the fenced area so, although they comprised a proportion of the sight count total, they were never available for capture.

Non-capture sampling of marked rabbits has also been used by Southern (1940) and Dunnet (1957c) to increase the accuracy of estimates, by eliminating error due to heterogeneity in trap response among individuals or

different segments of the population. Bouffard and Hein (1978) found that such heterogeneity affected the estimate of the number of individuals in the zero-capture class and limited the use of the Jolly-Seber model based on captures only.

Both Manly (1971) and Roff (1973a) point out that the accuracy of variances given by the Jolly-Seber model is highly correlated to the parameter estimates that they relate to. Consequently, underestimates of the population size may appear more accurate than they really are, and vice versa for overestimates. Logarithmic transformations have been suggested to overcome this problem. Although in this study the Jolly-Seber model consistently underestimated population size, the variances were comparable to those calculated from the sight counts.

Results from the frequency of capture methods used to estimate the mean standing population for the total duration of the study varied widely. The geometric distribution gave the best fit to the observed data, including when the population was divided into its male and female components. The other methods underestimated the zero-recapture class because the trappability of some rabbits was so high. This heterogeneity among individuals has already been emphasized. The geometric estimate of population size was very close to the overall mean of the monthly sight counts.

The rate of tag loss could not have altered population estimates significantly, especially as rabbits which had lost their marks were often retagged. Geis (1955) found that tag loss was insignificant and did not cause problems for population estimates in his study of cottontail rabbits.

The effect of stress is evident from the comparison of capture methods. Disappearance rates were consistently higher for rabbits that had been dug out, and especially so if they were transported from outside the area. Age could have been a factor, as young rabbits predominated among those individuals that were dug out. Those burrows that were accessible for digging out were located mainly within the fenced area, and many were used as breeding

stops. Very few adults had permanent burrows within the area. Natural mortality rates among young rabbits are much higher than for adults (Tyndale-Biscoe and Williams 1955, Bull 1962, Gilbert and Myers 1981) and this could have contributed to the apparently high disappearance rates for dug out individuals. The method of capture did not appear to affect male and female rabbits differently.

The disappearance rate was also correlated to the index of predation by hawks. Young rabbits are considerably more susceptible to avian predation than adult rabbits (Calaby 1951, Dunnet 1957a, Gibb et al. 1978) and the months when the disappearance rate is highest coincide with the presence of young in the population. However, predation probably accounts for only a small proportion of juvenile mortality and the correlation between disappearance rate and predation is merely symptomatic of the high juvenile mortality rate. The consistently higher disappearance rate during the second year is associated with an overall higher population density. Consequent food shortages may have led to greater mortality or higher levels of dispersal away from the study area compared with the previous year.

10 INTRODUCTION TO THE NEOPHOBIA SECTION

10.1 Control of small mammal pest species

The term 'pest' describes a human construct rather than an ecological reality (Jones and Kitching 1981). Organisms are perceived as pests if they damage crops or other products, transmit or cause disease, or in other ways conflict with human needs or interests. The economic significance of pest species has led to a considerable volume of research in comparison with species of no economic significance.

Within the vertebrates, small and medium-sized mammals tend to be the best represented groups among all the species regarded as pests. Frequently, they have been introduced deliberately or accidentally into new environments where natural predators, competitors, and other regulating factors are absent. The tendency for members of this group of mammals to be r-selected (MacArthur and Wilson 1967) in comparison with many other vertebrates and the lack of natural controls has meant that these species often have severe and detrimental effects on their new environments. Modification of formerly diverse environments, especially the development of agricultural monocultures, has also caused some species to become pests. Although not as ubiquitous as the black rat **Rattus rattus** and the Norway rat **R. norvegicus**, two highly cosmopolitan species, the European rabbit is a widely distributed mammal pest (see section 1.1).

The introduction of natural predators and disease, trapping, poisoning, and habitat modification have all been tried in an effort to control small mammal pest species, often with no lasting or significant effect. Many other techniques, such as those used to control damage by insect pests (e.g. repellants and attractants, selection for resistant varieties, competitive displacement, and chemosterilants), are unsuitable for most mammal pests.

10.2 Research on rabbit control in Central Otago

Extensive studies in Australia during the 1950s and 1960s (e.g. Lazarus 1956, Carrick 1956, 1957, Rowley 1959, 1963a, 1963b, 1963c, Poole 1963a, 1963b, 1963c) provided the basis for improvements in the strategy and efficiency of rabbit control operations in both Australia and New Zealand. Results of initial enclosure studies (Poole 1963b), later confirmed in field trials (Rowley 1968), indicated that poisoning was more effective when carried out during the non-breeding season. Other research has enabled a better understanding of the effects of natural regulation factors and has provided a basis for integrating control measures with natural mortality factors. Many of the findings of these Australian studies have been employed in establishing rabbit control procedures in New Zealand.

Research on control techniques in the Central Otago region began in 1967/68 because of concern by the APDC at the high cost of control in this area. This research, carried out by Rabbit Research Group (MAF), concentrated on accounting for the decreasing success rates of rabbit control operations but did not investigate the problem of the economic viability of rabbit control in this region.

Initial observation trials (Bell 1969, Nelson and Powell 1970) suggested several factors that may contribute to low success rates of poison operations including poor bait production and distribution, and sublethal toxicity of many baits. Further work confirmed that aerial bait distribution was far from uniform and that this problem was accentuated by factors such as cross-winds and the uneven size and shape of baits (Godfrey 1973). This resulted in excessive amounts of bait in some areas and very poor cover in others, thereby preventing many rabbits from encountering baits.

Two further poison trials (Bell 1973, 1974) attempted to overcome the problem of poor bait distribution by using excess baits to provide ideal coverage of an area and ensure that toxic baits were available to all rabbits in the population. Both these trials used the standard practice of two

applications of non-toxic bait followed by the toxic bait. However, in the second trial two additional areas were poisoned using the 'one-shot' technique. This involved a single application of bait, consisting of an approximately 1:10 mixture of toxic and non-toxic baits. Both trials resulted in less than optimal kills, although the practice of providing non-toxic 'prefeeds' did result in a significantly greater number of rabbits killed compared with one-shot poisoning.

These trials led to the hypothesis (J Bell pers. comm.) that cautious behaviour towards baits by rabbits was responsible for poor success rates of control operations and that this was partially overcome by one or more prefeeds of non-toxic baits. Prefeeds enable rabbits to encounter baits and become familiar with baits as a food source. This hypothesis was explored further in a subsequent poison trial (Bell 1976) which evaluated a control operation in which seven prefeeds at weekly intervals preceded the toxic bait application. The proportion of the population consuming baits rose to 80% by the fourth prefeed, but this subsequently declined and only 40% of the population were killed in this trial. Therefore, increasing the number of prefeeds did not improve the poisoning success and it was concluded that individual behaviour differences within the population were the cause of the poisoning failure (Bell 1976).

Results of the two earlier trials (Bell 1973, 1974), summarised in Table 10.1, had already established that rabbits which survived poison operations did not consume non-toxic bait either. This was established by dyeing the non-toxic baits with Rhodamine B which stains the mouthparts of rabbits feeding upon them. Following each of the trials a sample of poisoned rabbits was collected and a sample of survivors was shot. These rabbits were examined under ultra violet light for traces of fluorescing rhodamine to determine which rabbits had consumed non-toxic bait. Less than 2% of poisoned rabbits showed no traces of rhodamine indicating that very few poisoned rabbits failed to consume non-toxic baits. Similarly, among the survivors only a small

Table 10.1 Consumption of non-toxic bait by rabbits during prefeeds prior to poisoning (source: Bell 1973, 1974).

Trial	Poisoned rabbits R+	Poisoned rabbits R-	Survivors R+	Survivors R-	Percent kill
SJ6	242	0	3	60	75
SJ7	276	9	0	99	33-49 *

R+ = rhodamine-stained mouthparts, R- = unstained
* range of kills from parts of trial area

proportion had consumed non-toxic baits.

As a response to this apparently behaviour-based rabbit control problem the reintroduction of myxomatosis was proposed (Bell 1975) and alternative bait materials investigated (Ross and Bell 1979, Bell and Ross 1979). Until the present study no further work has been carried out on rabbit behaviour in relation to poison operation failures.

10.3 Neophobia

Research in Western Australia has produced similar evidence for behavioural changes in rabbit populations over the same period that changes in control operation success were occurring in Central Otago. During the periods 1958-62 and 1971-75 numerous trials were carried out to assess the effectiveness of one-shot poisoning using 1080 oats (Oliver et al. 1982). Indices of rabbit population size were determined before and after each trial. The results of these trials (Figure 10.1) confirm a decrease in the effectiveness of rabbit control operations over this period. The most rigorous comparison is (c) as both the earlier and later trials were carried out by the same operator (LAH), therefore highlighting the significance of the difference between the two sets of trials.

Selection for neophobic behaviour in rabbit populations as a result of repeated poison operations has been suggested as the most likely explanation

Source: Oliver et al. 1982

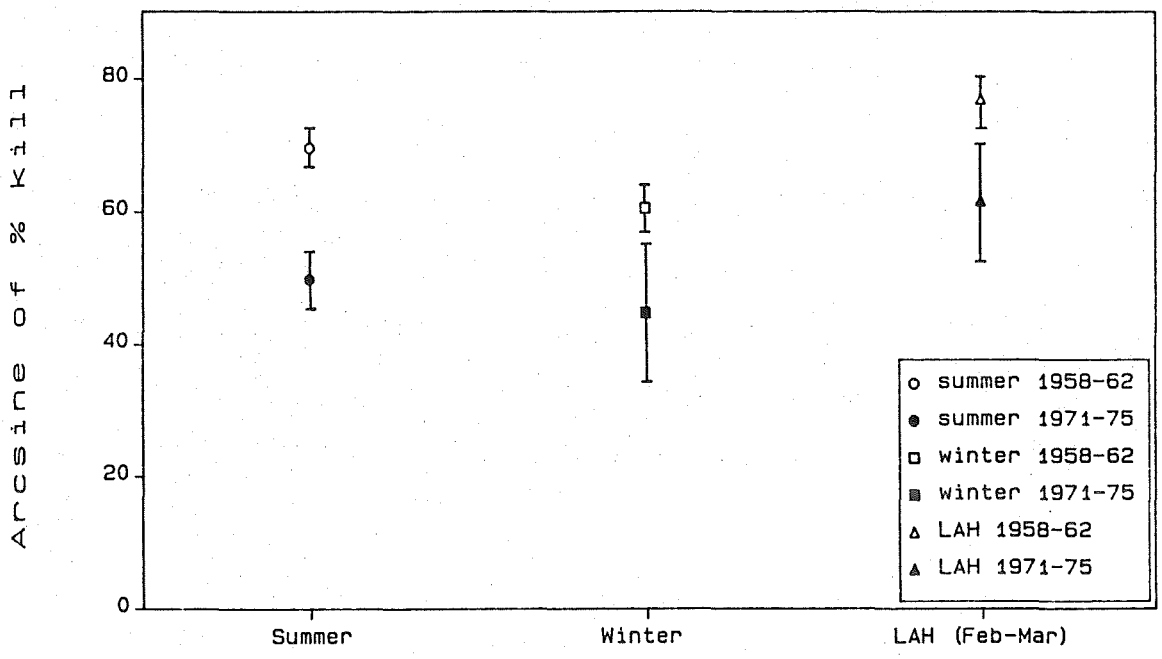


Figure 10.1 Comparison between the performance of compound 1080 (sodium monofluoroacetate) in 1958–62 and 1971–75 (means and 95% confidence limits).

for these results and the declining effectiveness of similar control measures in Central Otago (Bell 1979, Oliver et al. 1982).

Neophobia or "new object reaction" was first recognised by Chitty and Shorten (1946) in their study on Norway rats. Subsequently, this behaviour has been reported for many other species including black rats (Drummond 1960, Cowan and Barnett 1975), mice **Mus musculus** (Southern 1954, Wolfe 1969), voles **Microtis agrestis** (Shillito 1963), and deer mice **Peromyscus leucopus** (Sheppe 1966). The extent of neophobic reactions varies greatly between species and also within a species in different environments (Cowan and Barnett 1975, Barnett and Cowan 1976, Cowan 1977).

Selection as a consequence of control methods has been an important factor in the development of neophobic behaviour within animal populations. With its obvious survival value, neophobia is most highly developed in species commensal with man such as black and Norway rats (Barnett 1975) which have been continually subject to control measures. In contrast, two species within the same genus as black and Norway rats, **R. fuscipes** and **R. villosissimus**, do not exhibit neophobia (Cowan 1977). Both species rapidly investigated unfamiliar stimuli and this is thought to be the typical response to new objects and places by members of the genus **Rattus**. Both **R. fuscipes** and **R. villosissimus** are indigenous Australian species and have had little contact with man and, unlike black and Norway rats, have not been subject to extensive control measures.

Other forms of behavioural adaptations with survival value are known. Many species of herbivores avoid toxic plants unless driven by extreme hunger, a factor that can override basic avoidance patterns (Fowler 1983). Several species of rodents readily develop poison and bait shyness when subjected to control measures with acute poisons (Dubock 1982). For example, two species of gerbil (**Meriones hurrianae** and **Tatera indica**) develop long-lasting shyness towards both zinc phosphide poison and the bait materials used after only one or two sublethal encounters (Cowan 1978).

Another relevant adaptation is the high tolerance towards certain plant toxins by some mammal species. A notable example is the resistance to plants containing fluoroacetates by Western Australian populations of some herbivores. This tolerance appears to be an adaptation to the presence of monofluoroacetic acid in many species of the plant genera **Gastrolobium** and **Oxylobium**, which occur within the range of these mammals in Western Australia (Oliver et al. 1977, King et al. 1978). Populations of the same mammal species in most parts of eastern Australia, where these plant species do not occur, have correspondingly low tolerance to fluoroacetate compounds. Fluoroacetate tolerance has been used as a genetic marker to investigate the evolutionary history of some Australian mammals (Oliver et al. 1979). The evolution of genetic tolerance by some mammals (Howard et al. 1973, Oliver et al. 1977) has important ramifications for the suitability of 1080 (sodium monofluoroacetate) poison for the control of mammal pests in some areas.

Studies on the toxicity of sodium monofluoroacetate to rabbits in Western Australia indicate that no differences exist between populations of rabbits that are exposed to naturally occurring fluoroacetates and those from areas where these plants are not found (Wheeler and Hart 1979). Besides periodic poisoning using 1080, the added opportunity for selection for fluoroacetate resistance provided by the presence of plants containing fluoroacetate compounds could pose serious problems for current rabbit control methods in Western Australia. However, Wheeler and Hart (1979) suggest that poisoning techniques and the grazing characteristics of the rabbit reduce the selection pressure for the evolution of fluoroacetate resistance in Western Australian rabbit populations.

The situation with rabbits and fluoroacetates is not comparable with the genetic resistance of rat populations to anticoagulant poisons, in particular warfarin. The modes of action of fluoroacetates and anticoagulants are markedly different and selection mechanisms for resistance will differ. Therefore, evolution of genetic resistance to warfarin in the Norway rat

(Boyle 1960, Jackson and Kaukeinen 1972) cannot be used as direct evidence to predict similar changes within rabbit populations in relation to 1080 poison.

10.4 Objectives

This section reports results from three experimental field trials designed to determine the existence of neophobic behaviour in Central Otago rabbit populations. The preliminary trial (chapter 11) was largely aimed at checking techniques and procedures for the main poison experiment on the Butchers Dam population (chapter 12). Information from the Butchers Dam poison operation was of added value in that a considerable proportion of the population was comprised of 'known' individuals. Social status, social group structures, activity ranges, and movement patterns were well documented. This enabled an accurate assessment of the impact of social organisation on the outcome of the poison operation as well as investigating the responses of individual rabbits towards the furrow and baits. Chapter 13 contains the results of a second experiment on the Butchers Dam population designed to test the permanency of neophobic behaviour patterns. It examines whether changes in the social organisation of the population following a poison operation can induce changes in the propensity of individual rabbits to exhibit neophobic behaviour.

11 12-MILE BLOCK POISON TRIAL

11.1 Introduction

Observations during this small scale poison trial were designed to provide information on the way in which the behaviour of individual rabbits, and possibly neophobic responses, affected the chances of rabbits encountering and consuming baits. It was important to record the form of neophobic reactions towards the furrow or baits, and any other significant features of the rabbits' behaviour for reference during the main poisoning experiment on the Butchers Dam population.

The practice of presenting the baits in association with a furrow is widely used by the Alexandra Pest Destruction Board where access by four-wheel drive vehicles and motorcycles is possible. Australian research (Meldrum et al. 1957, Rowley 1957a) has indicated that a furrow provides continuity for the line of baits and greatly facilitates the rabbit's discovery of baits. Despite the belief that a freshly drawn furrow probably has an intrinsic appeal to rabbits, Carrick (1957) and Poole (1963b) observed that the initial response to the furrow was a typical "new object reaction" (Chitty and Shorten 1946) but that this response diminished after two or three nights. Nevertheless, Rowley (1957a) found that significantly more bait was consumed by rabbits where it was laid in association with a furrow compared with bait laid in scattered piles without a furrow. In addition, the furrow limited the area within which the rabbits' reactions to baits occurred and therefore facilitated easier and more reliable observations than would be possible if the baits had been applied aerially.

The degree to which rabbits are attracted to the furrow depends on how closely the furrow impinges on their existing feeding and movement patterns (Carrick 1957, Poole 1963b). Obviously, the best time for furrow poisoning operations is when territorial restrictions to movement are least, and when rabbits move over greater distances foraging for food. Unfortunately, these

two conditions do not always occur together.

The rabbit population on the small terrace chosen for this trial was ideally suited to observation. The terrace was almost completely surrounded by a series of rocky outcrops and it was possible to observe the population at close range, without disturbance, from a canvas hide placed above one of these outcrops. The terrace faced northeast and lost the sun earlier than the northwest-facing Butchers Dam study area. However, a large rocky outcrop sheltered the terrace from cold winds from the south. The vegetation cover on this area was similar to the Butchers Dam block but despite the apparent paucity of the habitat, rabbits did not appear to be under any food-related stress. The trial area has a history of regular control operations. Consequently, the selection pressure for neophobic behaviour towards poison baits has been considerable.

11.2 Results

Pre-poisoning observations over three days in June and July revealed that about 20 rabbits regularly frequented the terrace area. Regular scan samples of the terrace area at 10- or 15-minute intervals, for up to five hours each day, provided a series of counts of the number of rabbits present. Several rabbits had burrows on the actual terrace area, but most appeared to have permanent resting locations in the rocky outcrops surrounding the terrace.

As established from observations on the Butchers Dam population, rabbit numbers peaked in the hour around sunset. Rabbits made use of all parts of the terrace area and fed normally within the marked quadrats despite the presence of numerous wooden pegs. These pegs had been present for one month before the first observations were made. Although none of the rabbits were tagged, three individuals did have distinctive white patches of fur and could be easily identified during scan sampling.

Observations on seven days during August 1981 covered the poisoning phase of the experiment. Results from the four highest scan sample totals each day

indicate that a lower number of rabbits were active during August compared with the previous two months and the following month (Figure 11.1). It is unlikely that there was a decline in population size between July and August, so the decrease in the number of rabbits observed is probably due to changes in behaviour of individual rabbits. This is partly confirmed by counts on August 14, when a considerably higher number of rabbits were seen. This is associated with an earlier start time for observations on this day compared with other days in August.

Disturbance associated with the poison trial was considerable, with the drawing of the furrow and laying of the carrot baits by hand, and daily counts of the number of baits remaining. An effort was made to minimise disturbance by carrying out these tasks when rabbit activity was least.

During the first prefeed a decrease in the number of rabbits active within the quadrat zone compared with the previous two months was noted. In fact, following the laying of the first prefeed, very few rabbits ventured close to the furrow. Those rabbits that crossed the furrow while moving to another part of the area showed no reaction to it, although one rabbit did stop and sit beside the furrow for a short time. It was not until the following day that two rabbits were seen consuming baits. One individual fed for more than 30 minutes on baits, with brief interruptions between bouts of feeding. These interruptions occurred following threats from another rabbit. Several times the aggressor approached the rabbit consuming baits and threatened it, causing this rabbit to move away from the furrow temporarily. Each time the aggressor nibbled several baits before appearing to lose interest and move away.

During the first 24 hours only 7% of the carrot baits were consumed. A greater number were consumed during the following two days (Figure 11.2), but it was not until the fourth day that a significant disappearance of baits occurred. Bait-take was not evenly distributed among the quadrats; disappearance was faster within some quadrats than others, confirming

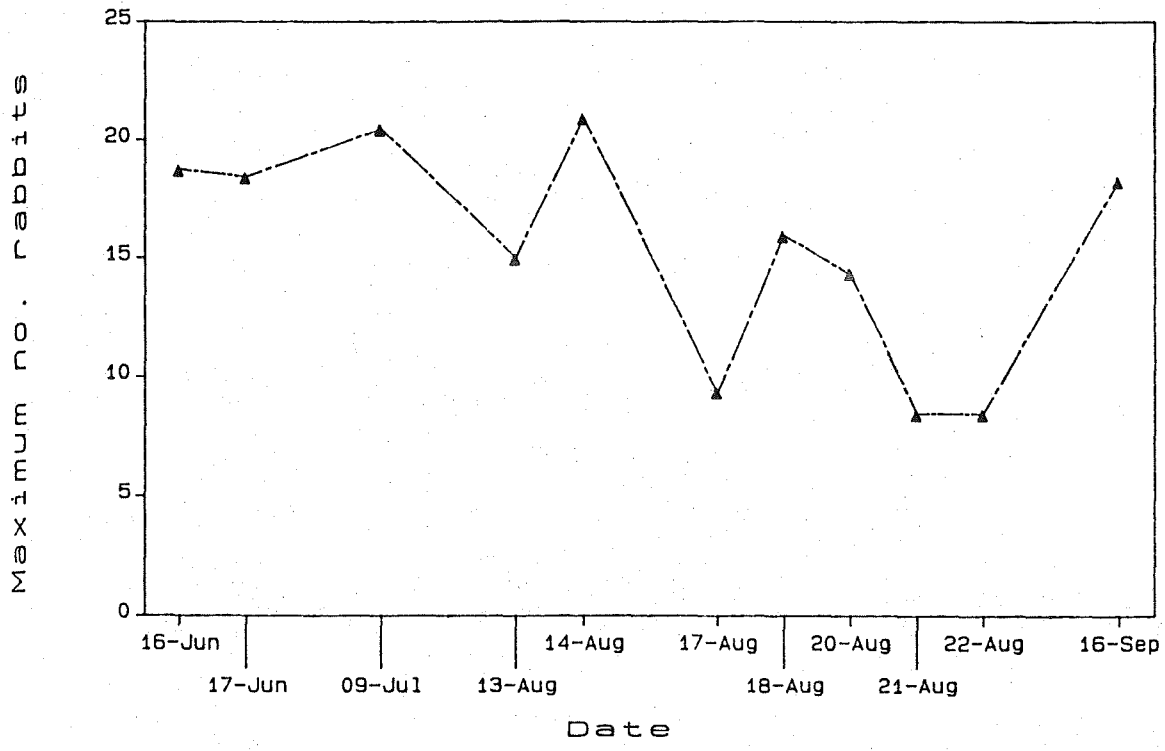


Figure 11.1 Level of rabbit activity indicated by sight count information before, during, and following the 12-mile block poison trial.

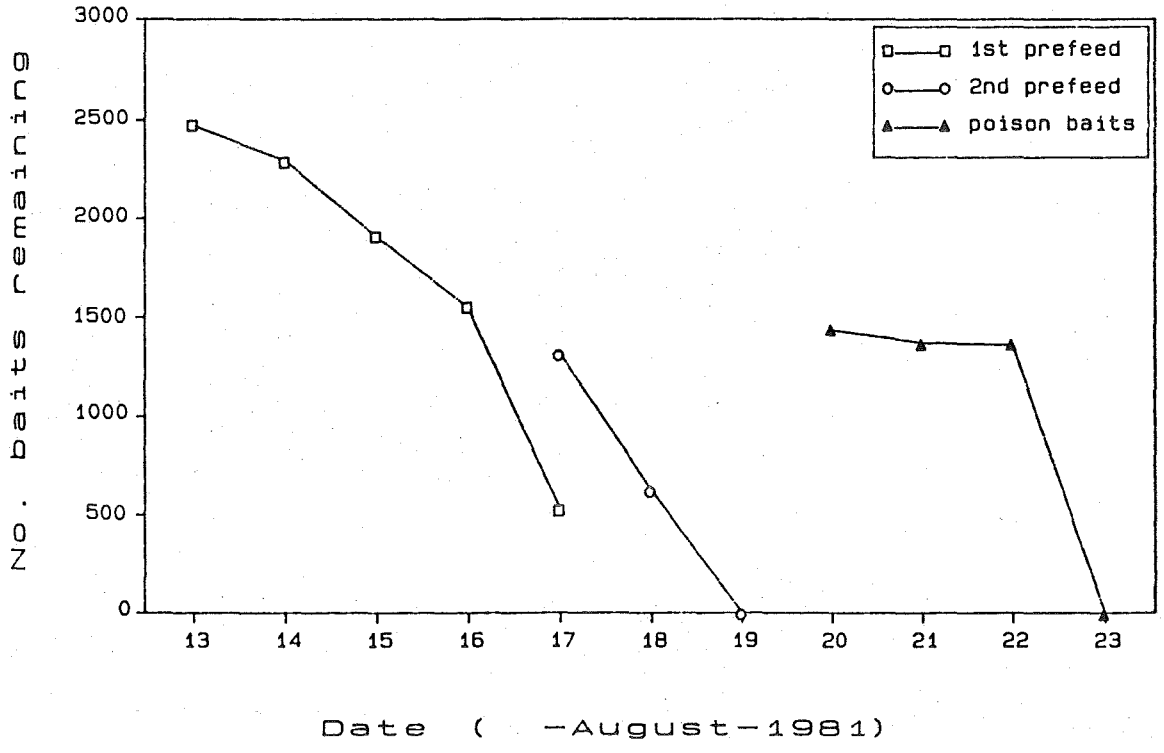


Figure 11.2 Bait disappearance patterns during the 12-mile block poison trial.

Carrick's (1956) suggestion that an increasing disappearance of bait is often due to increasing appetite of the same individuals.

By the fourth day several successive overnight frosts had caused the remaining baits to become rubbery and they had an unappetising appearance. These baits were removed and the second prefeed of freshly-cut carrot was laid. The total quantity of bait for the second prefeed was about 50% of the quantity laid during the first prefeed. A smaller quantity was used because of the slow disappearance rate and the weather conditions which were causing the baits to deteriorate rapidly. There were still sufficient baits (about 20 baits per metre of furrow) to allow each rabbit to consume carrot baits ad libitum.

The very low count for the number of rabbits active on the first day of the second prefeed is due to a much later start to observations that day. Only 90 minutes of daylight were available for observations following the distribution of the second prefeed. Therefore, not all rabbits had emerged during the shortened observation period following disturbance.

Disappearance of baits was much quicker than during the first prefeed. About half (53%) the baits disappeared within the first 24 hours and all baits had disappeared within 48 hours. Despite the lower quantity of bait laid, this disappearance rate seemed excessively high and was not supported by the low number of rabbits seen consuming baits during the afternoon observation periods.

Feeding and other activity within the quadrat zone remained low; very few rabbits were observed near the furrow. Most individuals who had been seen feeding within this zone in the preceding two months did not venture closer than 5 m from the furrow. The distinctively marked rabbits were among this group, so this observation was made with some confidence. However, the few rabbits that did consume baits appeared to do so regularly. They would feed in and around the furrow for considerable lengths of time. Often they moved along the furrow passing over some baits but stopping to consume others. Apart from

avoidance of the area around the furrow, rabbit behaviour, including feeding activity, appeared unaffected over the rest of the area.

Rabbits emerged later on the day the toxic baits were laid, although the total number of rabbits active eventually rose to a level similar to the previous days. The later onset of activity was probably due to disturbance from numerous passes overhead by an aircraft which was distributing non-toxic baits on an adjacent area. Toxic baits containing 0.02% 1080 were laid at a similar rate to the second prefeed (about 20 baits per metre). Rowley (1960) and Poole (1963c) have shown that a 1080 concentration of 0.02% is ideal and achieves high kills. Lower concentrations of 1080 give optimal kills only when natural food is scarce (Poole 1963b).

Most rabbits still appeared reluctant to venture near the furrow. Although several rabbits crossed the furrow during the observation period and two rabbits stopped and inspected baits for a short time, no rabbits were observed consuming toxic baits.

The next day observations began at sunrise. Besides three dead rabbits that were visible, all within 20 m of the furrow, several other rabbits were present on the trial area. Initially, the majority of these rabbits were feeding but by one hour after sunrise most rabbits were resting in warm, sunny locations. Following these observations, a search of the terrace and the surrounding area failed to locate any more dead rabbits. Late afternoon observations revealed that the three rabbits with distinctive white patches were still present, so had obviously not eaten toxic baits. During the pre-poisoning observations in June and July all three rabbits were observed feeding within the quadrat zone at some time.

Rabbit activity was similar the following day with most rabbits resting during the early morning period. Although another search was made following these observations, no more dead rabbits were found. A higher number of rabbits were visible during late afternoon observations, but again no individuals were seen consuming baits. No rabbit ventured into the quadrat

zone around the furrow; the closest individual fed about 10 m from the furrow.

Disappearance of toxic baits was very slow initially. During the first 24 hours only 4% were eaten with a further 1% disappearing in the second 24 hours. However, during the next 24 hour period nearly all remaining baits disappeared. The next search of the surrounding area revealed the reason for this significant and unexpected disappearance, and probably helps to explain the large reduction in the number of non-toxic baits during day four of the first prefeed and day two of the second prefeed (see Figure 11.2). Three sheep were found dead within 100 m of the terrace area. Several live sheep were also noticed, one of which appeared disorientated and was moving with difficulty. Although the 12-mile block had supposedly been cleared of stock prior to this trial, these sheep had either missed being mustered or reentered the area through a hole in the perimeter fence. The fact that these sheep had gone unnoticed during the previous days' observations was not surprising as the trial area was only a very small part of the 212 ha 12-mile block, which was characterised by numerous terraces and gullies.

Post-poisoning observations conducted the following month indicated that the number of rabbits on the terrace area was similar to the pre-poisoning level. No young rabbits were present so the increase following poisoning was attributable to an influx of adult rabbits from the surrounding area.

The degree of disturbance to the rabbit's behaviour caused by the poison trial was evident when the overall activity of the population is examined for the three phases of the experiment (Table 11.1). For the poisoning phase, only activity data recorded during the afternoon observation periods are included. As mentioned above, early morning observations revealed considerably less feeding and more resting compared with afternoon activity, and this would have exaggerated the difference between the three phases of the trial.

A lower level of feeding activity and an increase in the amount of resting and locomotory activity were associated with the poison trial. Similar changes in activity were not observed within the Butchers Dam population over

Table 11.1 Activity of rabbits during afternoon observations on the 12-mile block area for the three phases of the poison trial.

Behaviour category	Percent of observations		
	Pre-poisoning	Poisoning	Post-poisoning
Miscellaneous	–	–	–
Feeding	72.0	61.4	83.4
Grooming	3.9	3.0	2.8
Resting	15.9	22.1	8.8
Locomotory	5.6	7.7	1.7
Alert	1.0	1.3	1.1
Reproductive	.4	2.1	1.1
Territorial	–	0.6	–
Aggressive	1.2	1.7	1.1
Displacement	–	.1	–

the same period. In fact, feeding activity increased between July and August as expected with new vegetation growth at this time of year.

11.3 Discussion

Several interesting features of the rabbit's behaviour during a poisoning operation were observed. A distinct decrease in the level of activity, especially feeding activity, occurred in the vicinity of the furrow. Most rabbits which previously had used the area around the furrow rarely ventured within the quadrat zone during the poison trial.

Although several social groups (probably four) were present, restrictions on movement because of social group territoriality did not influence an individual's chances of encountering and consuming baits. Each group's range of movement incorporated part of the quadrat zone. In addition, the freedom of movement on the terrace area appeared to be greater than within the Butchers Dam population during the same months. The small size of the terrace area may have led to more contact between members of adjacent social groups, which resulted in greater tolerance towards individuals of other social groups.

Not only was activity in the region of the furrow and baits reduced, but the overall population level of activity decreased over the duration of the poisoning trial. A decline in the number of rabbits observed on the area occurred, as well as a decrease in the overall level of feeding activity. The factor responsible for this is probably the degree of disturbance associated with the poison trial and its effects on individual rabbits' behaviour. Most rabbits spent less time feeding and more time in resting and locomotory activity, as well as restricting their activities to parts of the terrace outside the quadrat zone.

Population density and food supply effects can probably be eliminated as factors contributing to the poor kill. The colder aspect of the trial area delayed the spring vegetation growth in comparison with the Butchers Dam area. This may explain why the increase in feeding activity associated with the spring flush of vegetation occurred about one month later than for the Butchers Dam population. The size of the rabbit population in relation to the trial area suggests relatively high grazing pressure; under these conditions acceptance of supplementary food (baits) should be good (Rowley 1963a).

Observations of the rabbits' reactions to the furrow and baits did not include all the responses to these objects recorded by Poole (1963b). The limited observation periods probably account for some lack of data but the fact that the reaction of most rabbits was characterised by a complete avoidance of the furrow and baits must also be considered. No evasive behaviour (Poole 1963b), where rabbits deliberately avoided crossing the furrow or if forced to cross it (e.g. while being chased) cleared it in a single frantic jump, was observed.

The behaviour of rabbits which did feed on baits was characteristic. Normally the first few encounters were brief with frequent sniffing of the baits and furrow, followed by nibbling at several baits. Usually the rabbit moved several metres from the furrow and grazed or rested for some time before returning to further investigate the baits and furrow. Subsequent encounters

were of greater duration and several baits were usually consumed before the rabbit moved away or further along the furrow.

Few instances of another rabbit interfering with an individual consuming baits were recorded. When interference did occur it was usually repeated several times over a short period, but such interactions did not appear to restrict an individual's ability to consume baits. In each case the aggressor quickly lost interest in monopolising the furrow area, or the rabbit which had been chased merely moved to another part of the furrow and continued to feed on baits.

Despite the paucity of direct observational evidence, a considerable proportion of the population avoided any contact with non-toxic and toxic baits through neophobic behaviour. The sustained cautious behaviour characterised by the complete avoidance of the furrow and baits by a large proportion of the population can be interpreted as an extreme form of neophobic response.

Based on a pre-poisoning population size of 22 rabbits, the reduction in numbers during the poison trial was between 14% (calculated from the number of dead rabbits recovered) and 50% (calculated from the maximum number of rabbits observed during the two days after the toxic baits were laid). The actual reduction was probably about 30-40%. Some rabbits may have died in their burrows or were removed by predators before they could be found. Meldrum et al. (1957) noted that the number of carcasses found on the surface varied between 30% and 50% of the numbers poisoned during a 1080 operation. Part of the decrease could be accounted for by rabbits becoming active after sunset or preferring to use surrounding areas for their daily activities rather than the terrace area during this period of considerable disturbance. Rowley (1968) carried out post-poisoning counts an hour later than pre-poisoning counts as it was thought that a reduction in competition arising from a decline in numbers may cause rabbits to emerge later.

The interference by sheep in this poison trial probably did not affect the number of rabbits killed; the toxic baits were present for at least 48 hours before the sheep began consuming them. Low bait disappearance during the second day combined with the failure to find any more dead rabbits confirms this suggestion. Some rabbits may have been prevented from encountering non-toxic baits during the prefeeds because of their premature removal by sheep, although observations suggest that this was unlikely.

As an attempt at control the trial could only be classed as a failure. This is confirmed by the post-poisoning observations, where less than one month later rabbit numbers were back to their pre-poisoning levels. The absence of young rabbits from September observations indicates that this increase is solely due to an influx of adult rabbits from outside the area, possibly accompanied by a return to the terrace area by some individuals which may have altered their activity ranges during the poison trial.

Poole (1963c) suspected that leaching of 1080 from baits combined with the small quantity of baits consumed by some rabbits may cause some individuals to develop bait shyness. Weather conditions during the trial combined with high soil moisture content may have caused some leaching of 1080 (Wheeler and Oliver 1978). However, it is unlikely that bait shyness contributed to the poor kill as those rabbits previously observed consuming baits ingested a number of baits during each visit to the furrow. Even allowing for some leaching, this feature of their feeding behaviour should have ensured that any rabbit consuming baits obtained a lethal quantity of 1080. Also, most toxic bait disappearance occurred during the first 24 hours when the effects of leaching would be least.

12 BUTCHERS DAM POISON OPERATION

12.1 Introduction

The control operation carried out on the Butchers Dam population was the most important part of this study. Unlike many previous studies on poisoning techniques which were carried out in experimental enclosures under quasi-natural conditions (e.g. Carrick 1957, Rowley 1957a, 1963a, 1963b, Poole 1963a, 1963b, 1963c), the present study involved a field population at a natural population density.

Although the Butchers Dam population had not been poisoned since 1973, it was subject to regular (almost annual) control operations prior to this (J Bell pers. comm.). Therefore, selection pressure for neophobic behaviour could have occurred, although somewhat less than the selection pressure acting on the more frequently controlled 12-mile block rabbit population. Despite an interval of nine years, and probably four to six generations of rabbits, between the last control operation and this experimental poison operation, it was expected that some rabbits would exhibit neophobic responses towards the furrow or baits. No negative selection pressure for the loss of neophobic behaviour would be expected in the absence of control operations over the previous nine years.

The poison operation followed existing Pest Board procedures. Several aspects of the operation were monitored, including bait quality, quantity, and distribution. This provided checks on various technical factors which have been partly responsible for control operation failures in the past.

Special emphasis was placed on recording the behaviour of rabbits in the vicinity of the furrow and baits, any reactions to these objects, and interactions between rabbits. However, normal transect and focal sampling continued to provide data for comparisons with previous months' observations. In this way, changes in the behaviour and movement patterns of rabbits during the poison operation would be easily identifiable.

12.2 Results

The poison experiment took place over a period of 17 days in August 1982, during which weather conditions were typical for that time of year (New Zealand Meteorological Service 1983). Maximum daily temperature on the study area ranged from 6.5°C to 16°C with ground frosts on four days. Daily minimum temperature was about 0°C on most days, although between August 20 and 25 the temperature fell below 5°C on only one occasion. Winds were moderate (3–5 on the Beaufort scale) and considerable cloud cover on most days contributed to high relative humidities. Apart from several light rain showers on two successive days (August 17 and 18) conditions were ideal for a poisoning operation.

Social group structures were well defined within the population, which contained 50–60 rabbits. Most individuals restricted their activities to their respective group territories (see section 7.2.5), although the level of reproductive activity was lower than the corresponding period the previous year. No young rabbits were observed on the area during August. The proportion of ground cover consisting of live vegetation in winter 1982 (15.2%) was low compared with other seasons. Associated with this was a relatively low level of overall feeding activity, but browsing and scratch feeding activity were more frequent. Under these conditions of limited food supply, supplementary food in the form of carrot baits should be readily consumed (Rowley 1963a).

12.2.1 Bait quality, distribution, and disappearance

Two samples of bait from each prefeed and the poison feed were collected by passing a 600 ml container beneath the output augur of the rotary bait screen. These samples were frozen for several days before being thawed and weighed on a Sartorius balance to the nearest 0.01 g. For convenience, each pair of samples was pooled for analysis. Weight-frequency distributions for these samples (Figure 12.1) indicate that despite screening to remove the very small fragments of carrot ("chaff"), a considerable number (21.8–33.7%) of

baits weighing less than 1 g remained.

Bait weights ranged from 0.01 g to 10.04 g although the number of baits near these two extremes was not great. The proportion of baits in the 2-5 g range suggested for rabbit control operations in New Zealand (J Bell pers. comm.) varied from 24.2% on the first prefeed to 40.8% in the poison feed. Even fewer baits were near the 5 g optimum weight (less than 12% weighed 4-6 g) suggested by Rowley (1959) for Australian conditions.

Results of the weight-frequency distributions for the bait samples collected from the poison feed, together with the assumed toxic loading of these baits (0.04% 1080 or 0.04 mg/g of bait material), were applied to a method of analysis of "bait quality" developed by Batcheler (1980, 1982). This technique estimates the number of baits an animal must encounter and consume before the probability of death exceeds 99%. The derived quantity (theoretical number of encounters) is termed the 99% bait quality index (99BQI).

Data on the proportion of baits in each weight class are combined with estimates of the quantity of 1080 contained in a bait of mean weight for each weight class (Table 12.1). Because of the surface area-volume function and the considerable amount of intact epidermis on many baits of intermediate size, the quantity of 1080 contained in sprayed baits is not directly proportional to bait weight. The relationship is best described by a quadratic regression based on the cube root of weight (Batcheler 1982). The bait weight and toxicity values are applied to a series of 100 hypothetical encounters by rabbits of a specified tolerance to 1080. After each successive bait encounter the number of rabbits surviving is calculated. This process is repeated for survivors until mortality is at least 99%. Indices of bait quality were calculated for 1.5 kg rabbits of two tolerance levels, based on an LD50 of 0.6 mg 1080 (Rammell and Fleming 1978) and an LD100 of 1.05 mg 1080 (Rowley 1963a). Those which succumb to an LD50 may be described as 'median' rabbits, while those which require an LD100 are termed 'tolerant' rabbits (Batcheler 1982).

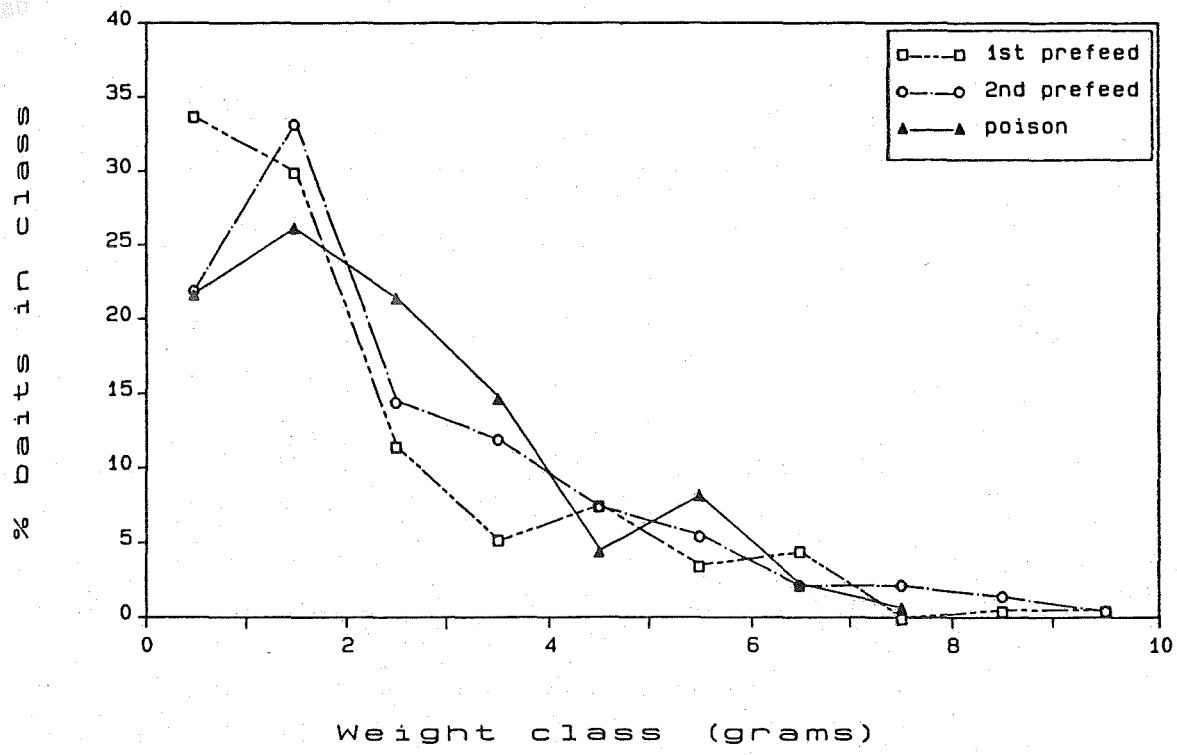


Figure 12.1 Weight-frequency distributions for bait material used in the Butchers Dam poison operation.

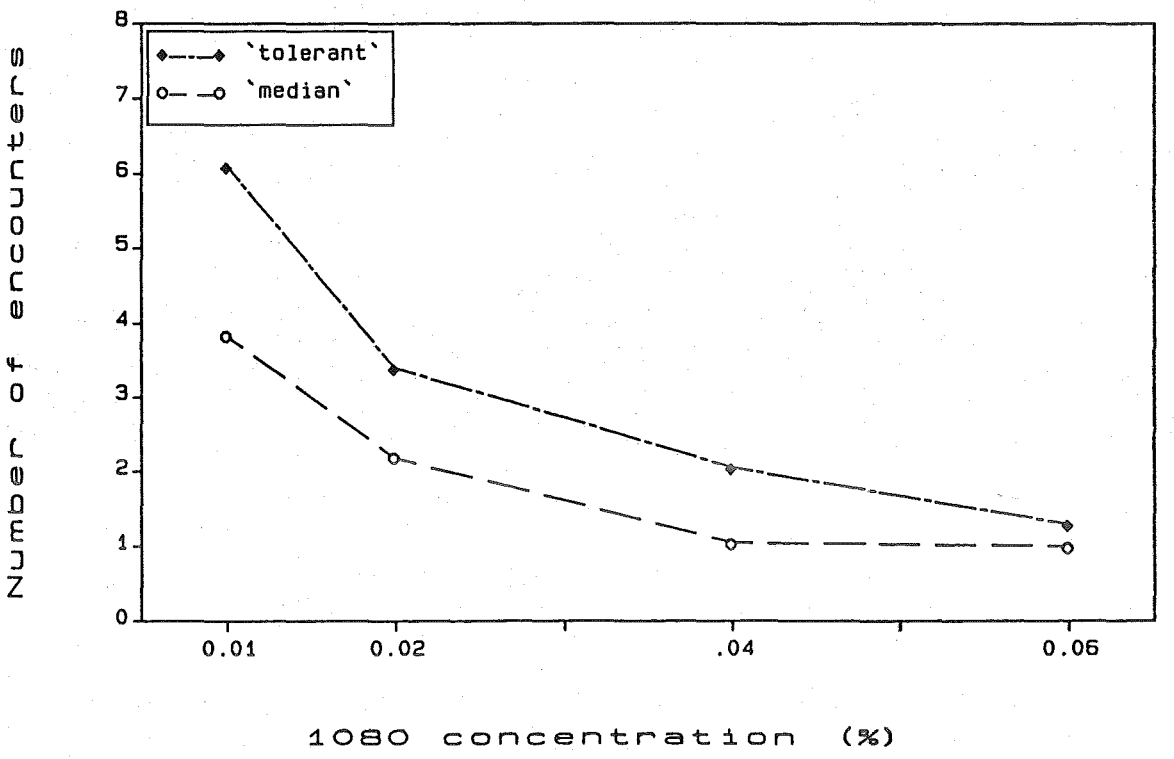


Figure 12.2 99BQI's for 1.5 kg rabbits of two tolerance levels based on an LD50 of 0.6 mg 1080 ('median' rabbits) and an LD100 of 1.05 mg 1080 ('tolerant' rabbits).

Table 12.1 Bait weight and toxicity data for the calculation of 99BQI values, based on an assumed toxic loading of 0.04% 1080.

Weight class (g)	Proportion of baits	Mean bait wt. (g)	1080 in bait (mg)
<0.25	0.022	0.20	0.22
0.25–0.5	0.059	0.40	0.38
0.5–1.0	0.141	0.71	0.57
1.0–2.0	0.259	1.53	0.91
2.0–4.0	0.363	2.83	1.28
4.0–8.0	0.156	5.39	1.95

At the assumed toxic loading of 0.04% 1080 employed in the poison operation, the 99BQI values were 1.05 encounters for median rabbits and 2.05 encounters for tolerant rabbits. 99BQI values were calculated for several other toxic loadings (Figure 12.2). Increasing the toxicity of the baits to 0.06% 1080 would not greatly affect the efficiency of a poisoning operation, as most median rabbits required only one bait at 0.04% 1080. The 99BQI value for tolerant rabbits declined from 2.05 to 1.31 encounters. At the normal toxic loading of 0.02% 1080 the 99BQI's were 2.19 for median rabbits and 3.40 for tolerant rabbits. Further reduction of the 1080 concentration to 0.01% results in an approximate doubling of the corresponding 99BQI values.

With the exception of one 20 m bait line, all furrow and baits were located inside the fenced area. The need for accurate observations during the poison operation and the higher proportion of marked individuals using the area inside the fence helped determine the placement of the furrow and baits. The furrow was drawn using a plough towed by a Land Rover but the baits were laid by hand to ensure an even distribution.

Bait distribution and disappearance were monitored by daily counts of the number of baits remaining in each of the 14 permanently marked 5 m plots. Bait count data for each plot are given for the three bait applications in Appendix 2. Initial bait distribution was relatively uniform (coefficients of

Table 12.2 Mean bait weight and bait application rates during the Butchers Dam poison operation.

Bait application	Mean no. baits per 5 m plot	Mean bait weight (g)	Bait weight per ha (kg)
First prefeed	120.14	1.99	11.95
Second prefeed	119.21	2.40	14.31
Poison feed	105.29	2.39	12.58

variation for the three bait applications of 7–20%) with the mean number of baits in each 5 m plot ranging from 105 (poison feed) to 120 (first prefeed). Rates of bait application for the three stages of the operation (Table 12.2) were reasonably similar and close to the desired level of 12.5 kg per ha.

Disappearance of bait occurred slowly in most plots over the initial 48 hours of the first prefeed. During this period numerous baits had been nibbled as though rabbits were 'testing' this new food source. After 48 hours the rate of bait disappearance increased markedly with considerable quantities consumed during each successive 24 hour period (Figure 12.3). Disappearance of carrot baits from the bait lines in grid squares P6 and A5 occurred more rapidly than from any other part of the area despite the fact that these bait lines were laid 24 hours after most of the first prefeed. More than 99% of all baits in grid squares P6 and A5 disappeared within three days of being laid, compared with five and six days for all other plots.

A high rate of bait disappearance continued throughout the second prefeed. During the first 24 hours 38% of baits were eaten, with a further 42% consumed in the second 24 hours. Plot counts on the third day revealed very few (less than 1%) baits remaining. Whereas the second prefeed was laid immediately following the disappearance of the last few baits of the first prefeed, there was a delay of 24 hours between the complete disappearance of the second prefeed baits and the distribution of the toxic baits.

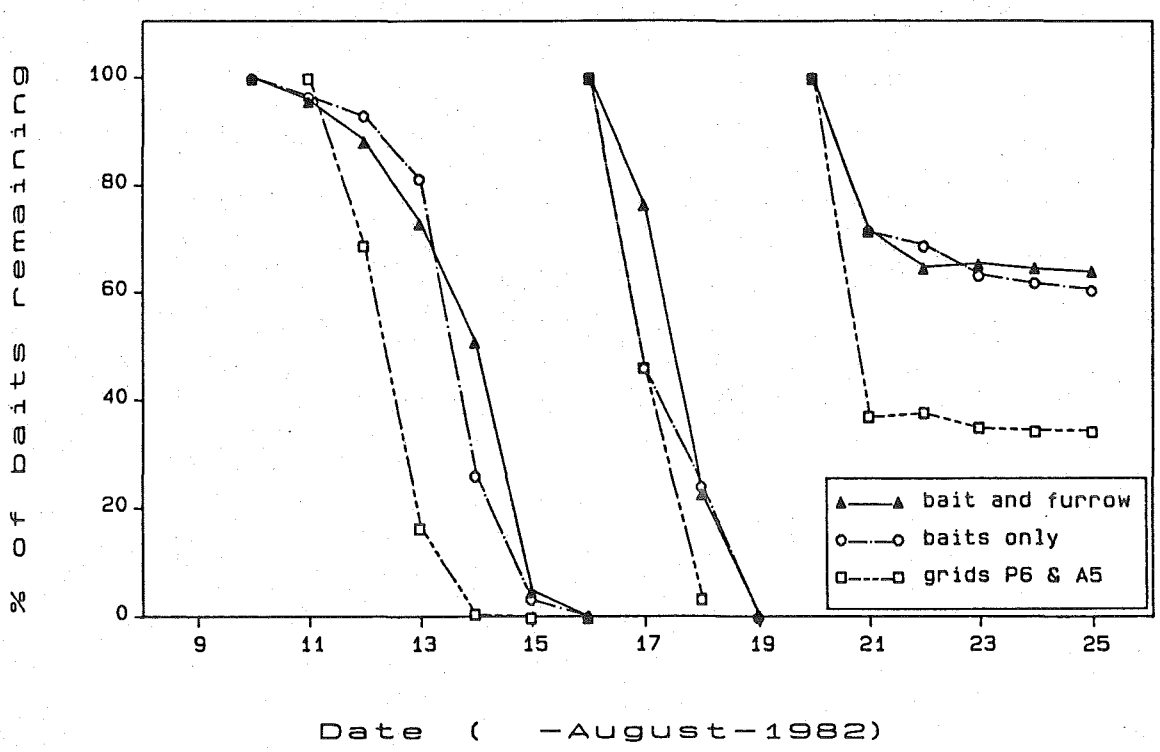


Figure 12.3 Bait disappearance patterns during the Butchers Dam poison operation.

A considerable number (34%) of toxic baits were consumed within the first 24 hours, with only a further 4% disappearing during the second 24 hour period. Thereafter the disappearance rate was minimal. Variation in bait disappearance rates between different plots was considerable. Disappearance rates varied from 10% in grid square M10 to 80% in grid square P6. Higher disappearance rates corresponded with areas of greater rabbit activity and frequent observations of bait consumption during both prefeeds.

Based on the quantity of bait removed and an estimate of the number of rabbits killed during the poison operation, bait consumption per rabbit can be calculated. Assuming 45 rabbits were killed (see section 12.2.4) and about 40% of the toxic baits were consumed (see Figure 12.3), each rabbit must have eaten about 90 baits. With a mean weight of 2.39 g for the toxic baits, this suggests that more than 200 g of bait material was consumed by each rabbit. However, an examination of stomach weights and contents from a sample (n=10) of the rabbits killed during the operation does not support this estimate. Stomach weights for these rabbits ranged from 91 g to 168 g, while visual estimates of the proportion of carrot bait in the stomach contents (excluding soft faeces) varied between 10% and 80% (average approx. 50%). Despite the marked difference between these two results, most rabbits obviously ingested many times the quantity of bait material required for a lethal dose of 1080.

12.2.2 Behavioural responses to the furrow and baits

Observations during the poison operation revealed a variety of reactions to the furrow and baits. These responses ranged from complete and almost immediate acceptance through indifference to complete avoidance. In addition, the reactions of some rabbits to the furrow and baits changed over the duration of the poison operation.

Simplistically and in retrospect, rabbits who had an opportunity to encounter baits were classified as either 'bait-takers' or 'bait-avoiders'. Obviously, bait-takers could be confirmed from the outcome of the poison

operation. This was useful in the case of several rabbits for whom observations of bait encounters were lacking or inconclusive. Membership of the bait-avoider category was determined mainly by direct observation but in some cases from movement and activity range information combined with the results of the poison operation. Data from previous months' observations confirmed that all rabbits that frequented the fenced area should have encountered baits.

A number of marked rabbits whose activity ranges did not extend inside the fenced area or include grid square P6 did not have an opportunity to encounter baits. This included M26, M73, and F88 (social group A3), M41 (a satellite attached to social group A3), M35 and F23 (social group A6), F70 (social group A4), F84 and F87 (social group A5), and F91 (social group A9). However, several of these rabbits (M73, F70, F87, and F91) were observed inside the fenced area during the previous month. Subsequent changes in their activity ranges may represent a response to the disturbance associated with the poison operation. Such changes in activity ranges could be interpreted as neophobic responses. However, this is largely a circumstantial conclusion and the changes noted in activity ranges may have been caused by other factors.

In addition to a decrease in the total number of marked rabbits observed inside the fenced area during August, several other effects were associated with the poison operation. The level of activity inside the fenced area was considerably lower than during the corresponding period in 1981 (Table 12.3). Whereas a marked increase in the number of observations occurred between July and August in 1981, a similar increase was not evident in 1982. Although the lower number of different individuals observed inside the fenced area accounts for some of this difference, many rabbits who previously concentrated their activities almost exclusively within the fenced area were often observed outside this area during August 1982. The relatively low level of activity inside the fenced area continued in September and October but this may have been due to the reduced population size following the poison operation.

Table 12.3 Level of activity inside the fenced area between July and October for 1981 and 1982.

Month	Percent of transect observations 1981	1982
July	34	32
August	52	31
September	58	39
October	57	38

Although sight count maxima from transect samples reveal that the same number of rabbits were present in July and August, emergence occurred slightly later in August even allowing for the difference in sunset times. Daily emergence times also exhibited more variation during the poison operation compared with the preceding months. The level of alert behaviour did not differ markedly from other months. However, the frequency of territorial behaviour did increase (see section 12.2.3).

Furrow and baits were located within the activity ranges of the majority of the population on the study area (including most of the marked rabbits). Therefore, based on the distribution of the carrot baits and the quantity used, it is safe to assume that all these rabbits encountered furrow or baits over the duration of the poison operation. Information about this group is summarised in Table 12.4.

Although nearly 70% of the rabbits in this group were classified as bait-takers, there was considerable variation among these individuals in terms of their responses to the furrow and baits. A few rabbits explored the furrow and consumed baits within the initial 24 hours of the first prefeed. Observations and bait disappearance rates suggested that most bait-takers consumed baits within the first 72 hours of their initial distribution. However, some rabbits did not venture close to the furrow or consume baits until well into the second prefeed, at least one week after the furrow was

Table 12.4 Social group and status of rabbits who had an opportunity to encounter baits and their classification as 'bait-takers' (T) or 'bait-avoiders' (A).

Social group	Males	Social status	Classification	Females	Social status	Classification
A1	M42	D	?	F61	D	T
	M59	I	A	F53	?	T
	M68	I	A			
	M44	S	T			
A2	M23	D	T	F33	D	A
	M46	I	T	F69	S	T
A3				F5	S	A
A4	M56	I	A	F51	D	T
	M60	S	T	F49	I	A
				F64	S	T
				F41	Sat	T
A5	M37	D	T	F42	D	T
	M40	S	T	F36	I	A
				F24	S	T
A6				F52	I	T
A7	M76	D	T	F65	?	A
	M47	I	T	F177	S	T
A8	M71	D	T			
	M51	I	A			
–	M78	?	T			
	M157	?	T			

D = dominant, I = intermediate, S = subordinate, Sat = satellite

drawn and the first baits laid.

In general, even bait-takers appeared wary of the furrow and baits at first. Disturbance associated with the drawing of the furrow and laying of the baits could help to account for some of the reactions recorded. Several rabbits whose previous range of movement was restricted to the fenced area were observed outside the fence frequently during August. This group included M23 and M46, both of whom had permanent resting locations inside the fenced

area. During the initial 48 hours of the first prefeed M23 and M46 spent most of the afternoon activity period outside the fence line. Eventually, they entered the fenced area but appeared nervous, moving about and changing their activity frequently. At one stage several rabbits, including M23 and M46, were seen fleeing from the area for no apparent reason. Most of these rabbits returned within 10 minutes.

Soon after returning inside and while chasing another rabbit M23 encountered the furrow and baits for the first time. During the chase the other rabbit crossed the furrow. On reaching the furrow M23 stopped abruptly and moved slowly along beside it. M23 then sat beside the furrow for about one minute before moving away to graze. After several minutes M23 returned to the furrow and moved along it, frequently sniffing at the ground and baits. This continued for several minutes before M23 moved away again. No consumption of baits was recorded during these initial encounters with the furrow. Several minutes later M46 similarly explored the furrow but again no baits were eaten. An initial 'exploration phase' was characteristic of many rabbits' responses to the presence of the furrow and baits within their activity ranges. The lack of observations of bait consumption in the initial 24 hours of the first prefeed is confirmed by the low bait disappearance (3.6%) during this period.

Most bait-takers were observed consuming baits during the second prefeed. By this stage the furrow and baits had been 'accepted' by many rabbits. These individuals would enter the fenced area soon after emergence and immediately move to the furrow and begin to consume baits. Rabbits often fed on baits continuously for 10 or 20 minutes before moving away to graze. Bouts of feeding at the furrow or bait lines usually occurred several times during each day's observation period. During extended periods of feeding on baits some rabbits would move along beside or in the furrow consuming some baits and passing over others. This was common during the initial stages but as the operation progressed most rabbits began to consume all baits in their path as they moved along the furrow. This led to parts of the furrow being cleared of

baits while other parts were relatively untouched. This is reflected in bait count data from the 14 permanent 5 m plots (see Appendix 2).

Several rabbits in the bait-taker category were never seen actually consuming baits. However, most of these individuals were observed close to the furrow or bait lines on numerous occasions. Checks under ultra violet light of the dead rabbits collected following the poison feed revealed signs of rhodamine on all of them. Therefore, all poisoned rabbits had previously consumed non-toxic carrot baits.

No sustained adverse reactions to the furrow or baits were exhibited by rabbits in this group, although several isolated instances of 'neophobic-type' behaviour were recorded. Such nervous reactions to the furrow and baits rarely persisted among bait-takers. On one occasion F51 inspected the furrow closely for several minutes seemingly unperturbed, whereas during her next encounter with it (about 60 minutes later) F51 crossed the furrow with a single large leap and moved quickly away. On most occasions F51 simply loped across the furrow with no apparent reaction to it. F42 was the only rabbit in the bait-taker category never observed inside the fenced area even though she was regularly observed during the 12 days prior to the poison feed. This suggests that the area inside the fence line was part of F42's nocturnal activity range, when more extensive movements are known to occur (Gibb et al. 1978).

An interesting feature related to the amount of rabbit activity near the furrow and baits was the degree of 'padding down' in and around the furrow. After the furrow was drawn, the soil thrown to the sides was soft and broken. During the first few days of the operation signs of activity around the furrow were clearly marked where this loose earth had been trampled by rabbits. As the operation proceeded the furrow and the area around it became well worn, with the result that by the time the toxic baits were laid all areas of baited furrow were well padded down. Significantly, there was considerably less evidence of rabbit activity in or around areas of unbaited furrow. Also, all instances of chinning and scraping in the furrow were recorded in regions

where bait was present.

Observations on those rabbits that survived the poison operation, the bait-avoiders, were difficult to obtain. Most individuals in this group avoided all contact with the furrow or bait lines and, consequently, very few close encounters were recorded. A range of reactions to the presence of the furrow and baits were evident, but unlike bait-takers, individual responses changed little over the duration of the operation.

Considerable changes in the activity ranges of some rabbits took place during the poison operation. These changes are most evident from the proportion of time certain rabbits spent inside the fenced area during August compared with the preceding and following months (Table 12.5). Considerable decreases in the amount of activity within the fenced area during August were noted for F33, F36, F49, M51, M56, and M59. A smaller decrease was recorded for M42 who disappeared completely from the observable area during the second prefeed. Similar changes in the activity ranges of some bait-takers were noted, although these were mostly restricted to the initial stages of the poison operation.

Table 12.5 Percent of activity inside the fence line for rabbits in the 'bait-avoider' category, for the months July to October.

Rabbit	Percent of transect observations			
	July	August	September	October
F5	15	13	45	51
F33	91	38	70	81
F36	25	7	65	30
F49	57	15	48	85
F65	83	87	93	89
M42	78	60	–	–
M51	90	17	83	85
M56	93	60	79	44
M59	33	20	6	32
M68	31	29	80	100

The observed shifts of activity range obviously reduced certain rabbits' chances of encountering the furrow baits. Such avoidance behaviour was sustained throughout the poison operation by these individuals. However, observations during September indicated that except for M59, all rabbits had resumed their previous activity patterns in terms of the amount of time they spent inside the fenced area.

Despite the low level of activity inside the fenced area for rabbits in the bait-avoider category during August, a number of encounters with the furrow and baits were recorded. Several rabbits, including M59 and M68, exhibited distinctive neophobic responses during these encounters. Typically, they approached the furrow hesitantly and inspected it for several seconds before jumping back and running away as if alarmed. This response was recorded several times for M59 and M68 on a number of days. With few exceptions, the intensity of these reactions to the furrow and baits appeared constant over the duration of the operation. M59's activity within the fenced area was characterised by numerous movements and changes of activity. This apparently nervous behaviour was not reflected in M59's activity outside the fence line. Similar neophobic reactions towards the white plastic pegs used to mark the 5 m bait plots were also recorded.

Some rabbits always maintained a 'safe' distance between themselves and the furrow or bait line. While they were frequently recorded in the same grid as furrow and baits, F5, F33, and F65 were never observed closer than 3 m from the furrow. F36 and M51 also kept away from the furrow and baits until August 23, three days after the toxic baits had been laid. On August 23 both F36 and M51 were observed inspecting the furrow. In addition, F36 scraped and chinned in the furrow several times. Despite the presence of numerous baits in the areas inspected neither rabbit was seen consuming baits. Similarly, M59 scraped and chinned the furrow on August 23 but did not consume any baits. M59's behaviour on August 23 was markedly different from that displayed during previous encounters with the furrow. It appeared that the intensity of the

reactions towards the furrow and baits by a few rabbits was beginning to abate during the last few days of the operation. More important however, was the continued failure of these rabbits to consume baits. Although many of the smaller toxic baits appeared dehydrated and shrivelled by this stage, the larger baits were less affected. Therefore, a decrease in the palatability of the carrot baits can probably be discounted as the main reason for continued bait avoidance.

A total indifference towards the furrow and baits was exhibited by some rabbits including F49 and M56. Despite a decrease in their overall level of activity inside the fenced area, F49 and M56 regularly fed close to the furrow and crossed it numerous times during the poison operation. Neither rabbit reacted to these foreign objects in any way. Invariably, they loped casually across the furrow in contrast to many other rabbits, including some bait-takers, who crossed the furrow in large leaps as if afraid of it.

M42's classification is unclear due to his disappearance during the early stages of the poison operation. The dominant position held by M42 was unlikely to have been usurped by either of the intermediate males (M59 and M68) in social group A8, thereby causing M42 to move away. The most plausible explanation for M42's disappearance is an adverse reaction to the disturbance during the poisoning operation although predation is another possibility. A complete shift of activity range away from the observed area was the most extreme form of response observed for those rabbits which decreased their activity within the fenced area (e.g. F33, F49, M51, and M59).

12.2.3 Observations on poisoned rabbits

Symptoms of 1080 poisoning were noted for a number of rabbits. Most of these rabbits had been observed consuming toxic baits for 10-30 minutes continuously. No signs of distress such as squealing or violent convulsions were noted. Instead, those rabbits which were observed after ingesting toxic baits appeared to eventually lapse into a comatose state. The first signs of

poisoning sometimes appeared about 30 minutes after the ingestion of toxic baits, but a latent period of 60-90 minutes was more common. Rabbits usually appeared uneasy, frequently changing from a resting position to some other activity. Many of the resting positions adopted appeared awkward as though the rabbit was not fully coordinated. Although some rabbits behaved normally for up to 60 minutes after consuming toxic baits, most were either comatose or behaving erratically after 90 minutes. The somewhat unusual behaviour of poisoned rabbits did not appear to affect the behaviour of other rabbits nearby. During trials on the toxicity and acceptability of a number of poisons, Lazarus (1956) found that the time to death following orally administered doses of 1080 varied from 1-5 hours. The effects of 1080 through its interference with the normal functioning of the Krebs cycle are variable. However, in rabbits and other herbivores death is generally the result of cardiac failure (Rammell and Fleming 1978).

12.2.4 Social organisation effects

Some rabbits from each social group that occupied space inside the fenced area were killed during the poison operation (Figure 12.4). Individual social group losses ranged from 50% (3/6, group A1) to 80% (4/5, group A5), with most groups losing about two-thirds of the individuals who frequented the fenced area. In addition, two other rabbits were known to have encountered baits although they belonged to social groups whose range of movement did not include any part of the area inside the fence line. However, these two rabbits (F5 and F52) had previously belonged to social groups A4 and A2 respectively and were familiar with the area inside the fence (see section 7.2.5). Despite hostile reactions from other rabbits, F5 and F52 continued to frequent parts of their former activity ranges each month. F52 was a bait-taker whereas F5 avoided contact with the furrow and baits whenever she was inside the fenced area.

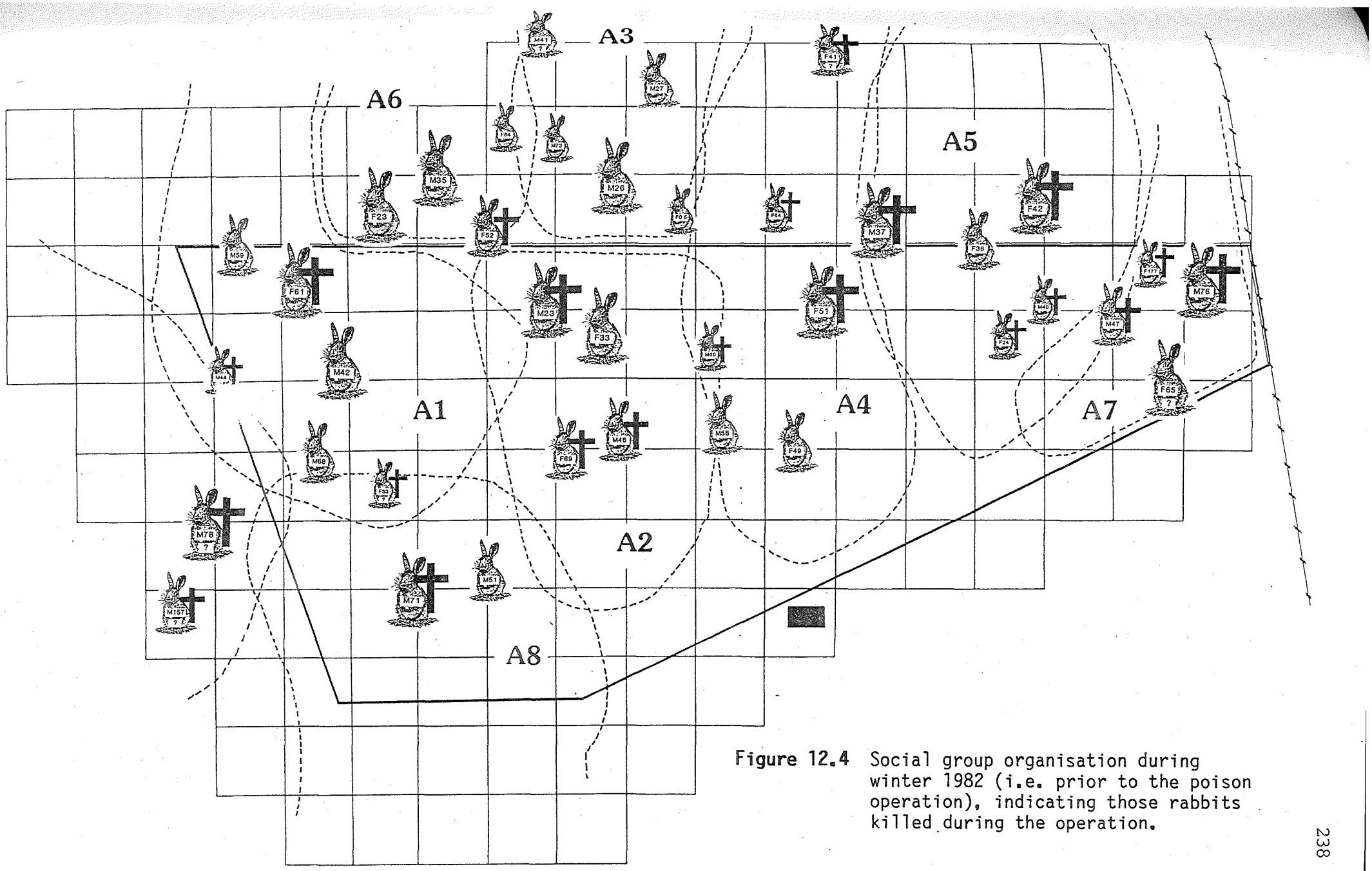


Figure 12.4 Social group organisation during winter 1982 (i.e. prior to the poison operation), indicating those rabbits killed during the operation.

Although their social group territories extended inside the fenced area, F84 and F87 from group A5, and F70 from group A4 were never observed inside the fence line. Each of these subordinate females had frequented the fenced area in the previous months, but activity inside the area was the exception rather than the rule. F84 and F87 were last seen inside during June 1982, while F70 was observed inside only on three occasions during the previous two months. With their low social status, these rabbits were often the focus of aggressive behaviour by other rabbits in their social groups. This probably caused them to frequent the least used parts of their respective group territories.

Numerous social interactions caused by the presence of the furrow and baits were observed during the poison operation. The most common interaction was aggression between two rabbits from the same social group. Most aggressive encounters involved male rabbits and occurred when a dominant individual noticed a rabbit of lower social status feeding on baits. The dominant individual usually threatened or chased the other rabbit from the furrow or bait line. Almost invariably, the other rabbit would return to the furrow or bait line and continue feeding but at a safer distance from the dominant rabbit. In some cases a return elicited further threats or chases, but more frequently the rabbit was able to feed undisturbed. Similar aggression by female rabbits was not recorded, although females were sometimes the object of aggression by dominant and intermediate status males.

By the time of the second prefeed a number of rabbits were exhibiting territorial behaviour around the furrow. This was noted for both male and female rabbits although, as expected, dominant males chinned and patrolled the furrow most frequently. Vigorous bouts of scraping in the furrow were also recorded on a number of occasions. This usually occurred where the ranges of adjacent social groups overlapped. Scraping could be a response to the olfactory signals (from faeces or chin gland secretions) of rabbits from a different social group, and was sometimes recorded as a prelude to chinning.

Preoccupation with feeding on carrot baits sometimes appeared to avert aggression between rabbits of different social groups. For example, several rabbits from social group A5 often ventured into the A7 group territory to feed at the bait line in grid square A5. In addition, rabbits from A7 extended their range of activity during August to include the bottom region of the A5 group territory where the furrow passed through grid squares C7 and D7. These extensions to previous movement patterns usually involved rabbits of low social status. The dominant M76 rarely tolerated rabbits of his own social group feeding on the bait line in A5 when he was present and always chased foreign rabbits from this area. However, on several occasions when M76 was absent rabbits from both groups fed together peacefully. Significantly, whereas all rabbits in the A7 social group extended their range of movement during August, even F65 who was a bait-avoider, the least change was shown by M76. The dominant M37 from group A5 was also more conservative than lower status rabbits from that social group.

12.2.5 Effect on the population

The presence of marked rabbits in the population was very useful when comparing various estimates of the proportion of the population killed during the poison operation. The most accurate estimate is likely to be that based on observations of marked rabbits only. From a total of 31 marked rabbits who were assumed to have encountered baits (see Table 12.4), 68% (21 rabbits) were killed. Although carcasses of only 15 tagged rabbits were retrieved, the other six rabbits were never seen again. Two of these, M40 and F24, were actually observed feeding on toxic bait on August 20.

Based on the number of marked and unmarked carcasses retrieved, and the number of marked rabbits assumed killed but not found, an estimate of a total of 45 rabbits killed during the poison operation was obtained. This number appears rather high in comparison with sight count data and the number of rabbits present on the area immediately following the poison operation.

However, sight counts during winter months probably tend to underestimate the actual population size because of a lower level of activity during these cold months. Whereas sight count maxima for spring, summer, and autumn months include nearly all rabbits present, a lower proportion of the total population were active on any given day during the coldest months.

Pre- and post-poisoning sight counts obtained from transect samples during August give an estimate of a 57% kill. The lower value for this estimate compared with that based only on marked rabbits is due to the inclusion of all rabbits on the observable area. Some of these rabbits never entered the fenced area or grid square P6 and, consequently, never had an opportunity to encounter baits.

When pre- and post-poisoning count data are obtained from July and September transect samples an even lower estimate of a 39% kill is obtained. The difference between this estimate and that based on August counts is partly due to the inclusion of new rabbits in the population observed in September. No young rabbits were seen in September so the increase noted between August and September transect samples is due to an influx of adult rabbits onto the observed area.

Considerable changes occurred in the social organisation of the population following the poison operation (see section 7.2.5). By September, many rabbits who previously had activity ranges outside the fence line had extended their ranges to include parts of the area inside the fence. Some shifts were also evident among the bait-avoiders from inside the area.

With the decrease in overall population size most rabbits extended their activity ranges (see section 8.2.4). Consequently, group territory size increased and overlap of adjacent group territories became greater. However, because of the smaller population size the greater overlap did not lead to more intragroup encounters and aggression between rabbits of different social groups. The basic trend was for rabbits to gravitate towards the areas of better food supply.

F33 resumed her previous pattern of behaviour and concentrated her activities in the A2 area. M26 from group A3 and M56 from group A4 also moved into the A2 area. This social group also contained a young subordinate male (M79) who was untagged before September. M26's shift enabled M35 to increase A6's group territory to include part of the former A3 group territory. In association with F23, M35 also extended the A6 group territory to include a region inside the fenced area between the A1, A2, and A8 group territories. The A1 group territory was relatively unchanged, possibly because this group was least affected during the poison operation. Similarly, social group A8's territory was little changed from the previous month, although M68 had left A1 and joined M51 in A8.

F5 and M73 moved into social group A4 where F49 was the only former member present. F36, F84, and F87 remained in group A5 although the activity ranges of F84 and F87 increased noticeably in the absence of F42 and F24. M67 who had been marked in January 1982 but not seen subsequently, returned to the observed area and assumed the dominant male role previously occupied by M37. M67 was able to exert his dominance over both the A4 and A5 social groups in a similar fashion to M37. M73 restricted his activities to the A4 group territory and never challenged M67's dominant position.

12.3 Discussion

The concentration of 1080 (0.04%) applied to the toxic baits in this experiment was twice the normal application rate used for rabbit control. This was mainly to ensure that baits remained lethal for longer after being laid (Staples 1968). Leaching of 1080 from baits following rain, frosts, dew-fall, or contact with wet soil (Griffiths 1959, Corr and Martire 1971, Wheeler and Oliver 1978) would not render baits sublethal as quickly as if an application rate of 0.02% was used. Although there were several rain showers during the second prefeed, conditions following the distribution of the toxic bait were ideal. There was no precipitation and very little dew-fall between August 20

and 25. Soil moisture content on the Butchers Dam study area was noticeably less than on the 12-mile trial area, mainly due to a sunnier and more exposed aspect. These factors suggest that leaching of 1080 from baits would have been minimal.

Although a considerable amount of chaff remained in the bait material distributed during this operation, the amount was significantly less than that obtained when a bait screen is not used. In two bait production trials using a Reliance bait cutter, Batcheler (1982) found that 62% and 87% respectively of all carrot fragments produced were less than 0.25 g (cf. 2.3-8.2% for screened samples collected during this operation). The weight-frequency distributions of the bait samples obtained during this operation are typical of mechanically screened material (see Figures 5 and 6 in Batcheler 1982). Manual sieving of the bait material had virtually no effect. Failure to remove all chaff during the screening of baits is probably due to fragments of carrot adhering together because of the wet surfaces of the baits after cutting. Production of large amounts of chaff is a characteristic of all types of carrot cutting machines. Batcheler (1982) found that removal of chaff by mechanical screens increased the average weight and the proportion of potentially lethal baits considerably. Although this involves some wastage of bait material, it significantly reduces the number of bait encounters required to obtain a lethal dose of 1080.

Freezing of the bait samples for several days prior to weighing did not appear to alter the weight-frequency distributions for the bait material. These distributions were almost identical to those obtained by Batcheler (1980, 1982) for fresh material weighed in the field.

Satisfactory distribution of bait was achieved by laying each bait application by hand; bait counts in marked plots confirmed the even distribution. As in the 12-mile block poison trial, disappearance of baits was slow at first but after about 48 hours considerable quantities of bait were consumed during each successive 24 hour period. Carrick (1957) and Rowley

(1957a) recorded similar rates of increase in bait consumption during their enclosure trials. However, the rate of bait disappearance can vary with season, weather conditions, and disturbance (Carrick 1957, Rowley 1957a). While it took six days for all the bait material laid in the first prefeed to disappear, the second prefeed was consumed in only 72 hours. No change in the rate of bait consumption was evident between the second prefeed and the poison feed.

Initial bait disappearance was relatively even over all areas of furrow and the bait lines. The high incidence of nibbled baits during the first 48 hours of this operation confirms Carrick's (1956) findings using non-toxic bait labelled with radioiodine. During Carrick's studies rabbits were captured and a Geiger counter was used to scan the thyroid region for radioactivity, the level indicating the relative amount of bait eaten by each rabbit. The presence of nibbled bait and very low radioactivity readings suggested that many rabbits typically 'tested' the bait material on their first encounter.

As the operation progressed and rabbits became more accustomed to feeding on baits, the pattern of disappearance became more patchy. This occurred because rabbits would move along the furrow consuming nearly all baits they encountered. In contrast to Rowley's (1957a) findings, consumption of baits from the bait lines proceeded at least as rapidly from areas of furrow. However, Rowley distributed baits in discreet piles so that the furrow actually provided continuity between successive piles of bait. Rapid disappearance of bait from the lines in grid squares P6 and A5 was due to the greater level of rabbit activity in these areas. Some individuals fed for periods of up to 20 minutes at the furrow or bait lines. This continued on the day the toxic baits were laid, leading to ingestion of large quantities of toxic material by many rabbits.

Evidence of the intrinsic appeal of the furrow (Rowley 1957a) was not clearly established. Rabbits which were not strongly neophobic rarely exhibited an attraction towards areas of furrow in their activity ranges

except to feed on baits. Unbaited furrow was largely ignored as evidenced by observations and minimal padding down of the loose soil in and around the furrow.

The reason for the discrepancy between the estimated bait consumption per rabbit determined from bait disappearance data and the actual amount consumed based on stomach weights and contents is unclear. Although smaller baits may have been preferentially consumed, biasing the estimate from the disappearance data, this is unlikely in view of Rowley's (1959) findings. Alternatively and more likely, bait disappearance rates from the 5 m plots could have been greater than the overall rate, but this was not checked. In addition, other animals including birds may have consumed bait material. Although no dead birds were found, as expected when baits are dyed green (Caithness and Williams 1971), at least one possum **Trichosurus vulpecula** was killed during the poison operation. Nevertheless, even if the lowest estimate is taken, the fact remains that most rabbits ingested several times the lethal dose of 1080. Observations of the feeding activity on the day the toxic baits were distributed confirm this. Where insufficient bait is distributed, excessive appetite by some rabbits may prevent others from encountering baits (Carrick 1956, Poole 1963b, Rowley 1963b). Studies on carrot bait consumption during prefeeds have revealed average per capita nightly consumption of almost 600 g (Rowley 1957a) and maximum daily intakes exceeding 900 g by some rabbits (Carrick 1957).

The amount of poison contained in a bait is a complex relationship between bait weight and surface area, and the absorptive characteristics of the bait which are partly dependent on the proportions of intact epidermis and parenchyma tissue on the bait surface (Staples 1968, Batcheler 1980, 1982). The indices of bait quality (99BQI's) calculated for the material and assumed toxicity used for the poison operation indicate that, on average, consumption of only two baits would result in a lethal dose of 1080 for most rabbits. In fact, based on Rowley's (1963a) LD50 of 0.6 mg 1080 for a 1.5 kg rabbit,

nearly 80% of the population would obtain a lethal dose by consuming a single bait. Successive reductions in 1080 concentration leads to an almost exponential increase in the number of baits required to ensure a lethal dose. At the normal concentration of 0.02% 1080 some rabbits would need to consume nearly four baits before a lethal quantity of 1080 is ingested. Any increase in toxic loadings above 0.04% 1080 would lead to little or no increase in the effectiveness of the bait material.

The implications for accuracy in the toxic loadings applied to bait material during large scale poison operations are obvious. Small errors in the quantity of 1080 used may lead to considerable decreases in the effectiveness of the bait material. This is especially relevant to aerial poisoning operations where bait encounter is a stochastic process, unlike operations where baits are distributed with a furrow. If several baits are required to kill an animal and various factors, including the onset of the effects of the poison, act to reduce the animal's frequency of bait encounters sublethal poisoning may occur. Provided that bait application levels are sufficient, such problems should not arise in rabbit control operations. However, as Batcheler (1982) points out, emphasis must also be placed on high standards of bait preparation in order to minimise the number of bait encounters required.

Although rabbits were classified as either bait-takers or bait-avoiders, a continuum of responses to the furrow and baits were recorded. Most bait-takers accepted these new objects within several days but a few rabbits took more than a week before they were observed near the furrow or consuming baits. Although Carrick (1957) found that the rate at which rabbits began to consume baits depended on how closely the furrow impinged on their existing feeding and movement patterns, variation during this operation was a clear indication of the differences in individual responses which existed, as the furrow and bait lines passed through the daily activity ranges of all rabbits who frequented the fenced area. Several instances of neophobic behaviour were observed for rabbits in the bait-taker category, but these were usually

isolated occurrences.

Bait-avoiders or neophobic rabbits exhibited a wide variety of adverse reactions to the furrow and baits. These ranged from almost complete avoidance and marked changes in activity ranges by some rabbits to mere indifference towards the furrow and baits by other rabbits. Relatively few instances of actual encounters with the furrow and baits leading to obviously neophobic responses were recorded. Limitations of the method and period of observation reduced the chances of viewing more encounters.

While the most distinctive neophobic reaction to the furrow and baits is an approach, followed by the rabbit jumping back and running away as if alarmed, it was not the most common response. Basic avoidance or indifference were more frequent. Nevertheless, each type of response represents a variation on the general neophobic theme. The important feature is that rabbits which regularly exhibited such behavioural responses failed to consume carrot bait.

Rabbits of most social status levels were represented within both the bait-taker and bait-avoider categories. Dominant and subordinate males were absent from the bait-avoider group but this could be an artifact of the limited sample size. Females of all status levels were included in each group. There was a tendency towards more bait-takers in the dominant and subordinate status levels, and more bait-avoiders among intermediate status rabbits. However, this may also be an artifact of the small sample size. The relative proportions of bait-takers and bait-avoiders were similar for males and females. Therefore, there is little evidence to suggest that rabbits of any particular sex or social status class are more likely to display neophobic behaviour.

There was no relationship between the trappability of rabbits and neophobia; despite the markedly greater trappability of female rabbits, the proportion of neophobic individuals was similar for males and females. In fact, the overall frequency of capture was slightly greater for bait-avoiders compared with bait-takers. Several bait-takers had been captured only once; in

contrast, three bait avoiders had been captured at least six times.

It is unlikely that any rabbit developed poison shyness during the operation. Compound 1080 is supposedly odourless and tasteless (Rammell and Fleming 1978) and it is relatively slow-acting (Lazarus 1956, Rowley 1963c, Rammell and Fleming 1978) so that a rabbit surviving a sublethal dose would be unlikely to associate any poison-induced anorexia with either the poison or the bait. However, results of recent bait acceptance trials (Morgan 1982) suggest that possums may survive poison operations through olfactory aversion. This casts some doubt on previous workers accounts of the properties of 1080. However, the concentrations of 0.1% and 0.2% 1080 used in the possum trials are markedly higher than the 0.02% concentration currently used for rabbit control operations.

Individual rabbits' responses changed little over the duration of the poison operation. No rabbits that had been regularly observed as bait-avoiders consumed toxic baits. However, there was some evidence that a few apparently neophobic rabbits had begun to accept the presence of the furrow and baits in the environment after about two weeks. This was not common, with the majority of bait-avoiders remaining neophobic throughout the entire operation.

Behavioural responses similar to most of those identified during this study have been recorded during experiments on poisoning techniques carried out in Australia (Carrick 1956, 1957, Rowley 1957a, 1958, Poole 1963a, 1963b). However, as Fennessy and Mykytowycz (1974) acknowledge, populations of mammals are characterised by a range of behaviourally different individuals. Responses to similar stimuli vary not only between individuals but also within a particular animal depending upon factors such as season, age, sex, reproductive state, and nutritional needs. This complexity of behaviour patterns helps to explain the continuum of responses exhibited by rabbits towards the furrow and baits, and the fact that in some cases behavioural differences between bait-takers and bait-avoiders were only subtle. Neophobia in rabbit populations cannot be categorised as a single, easily observed

characteristic but rather comprises a variety of responses. The common denominator among all rabbits exhibiting neophobic responses towards furrow or baits is that they cannot be killed using current poison control techniques.

Changes in environmental conditions (e.g. extremely limited food supply) may cause some variation in the level of neophobia exhibited within a population. Ground cover details for July 1982 indicate that the food supply was probably at a lower level than during the previous winter. This is confirmed by the greater frequency of browsing and scratch feeding in winter 1982. Under such conditions of food shortage, maximum effectiveness of control operations should be achieved (Foran et al. 1985). However, the existence of a relationship between poisoning success and fat-related condition, similar to that reported for possums (Batcheler et al. 1967, Bamford and Martin 1971), is questionable. Despite very low fat reserves during August 1982, a reflection of the limited food supply and the physiological state of individuals within the population, acceptance of alternative food (carrot baits) remained relatively low.

The effects of social organisation on the outcome of control operations was first outlined by Poole (1963a, 1963b). During the present study social interactions often interfered with an individual's bait consumption but due to optimal placement and quantity of baits provided, these factors did not affect the final outcome of the poison operation. Most interactions around the furrow or bait lines were typical intragroup dominance displays by higher social status rabbits towards intermediate or subordinate rabbits consuming baits. Intergroup encounters sometimes arose when rabbits from one group were attracted to baits in a neighbouring group's territory. In most cases rabbits chased from baits either returned and resumed feeding after a short period or moved to another part of the furrow or bait line. Therefore, the influence of social effects during the poison operation was minimal. However, in cases where bait distribution is patchy or sparse, as sometimes occurs during aerial bait distribution (Godfrey 1973), such factors may significantly affect the

success of the operation.

Despite an estimated 60-70% kill, the overall effect of the poison operation on the population was minimal. By the following month, movement of adult rabbits into the observable area had reduced the estimated effect of the control operation to less than a 40% reduction. Survivors either shifted their activity ranges towards more favourable parts of the area or increased the size of their activity ranges. The latter effect is probably a natural response to the decrease in population density (Myers and Poole 1959, 1961, Gibb et al. 1978).

13 GOLF BALL EXPERIMENT

13.1 Introduction

Several studies of neophobia in rodents have stressed the survival value of such behaviour (e.g. Chitty and Shorten 1946, Shillito 1963, Barnett and Cowan 1976). In order for neophobic behaviour to constitute an evolutionary stable strategy (ESS) (Krebs and Davies 1981) it must be maintained throughout an animal's lifespan. Although seasonal, social, and nutritional influences can produce variation in individual behaviour, these changes would not usually be expected to alter the animal's basic disposition for neophobia. Relative constancy throughout an individual's lifespan and between successive generations is strong evidence for the genetic basis of this trait.

Based on this premise, it was important to examine the reactions towards unfamiliar objects of those rabbits which survived the poison operation. For this experiment, golf balls were used instead of a furrow and carrot baits. Some of the rabbits examined were bait-avoiders while the remainder survived the poison operation in August because they never had an opportunity to encounter baits.

13.2 Results

By October, the rabbit population on the observed area had largely 'stabilised' following the considerable changes in social organisation and activity patterns resulting from the poison operation. The three sets of golf balls were placed in the area during the final two days observations in October 1982. Areas of relatively high rabbit activity inside the fence line were chosen as the sites for the golf balls. Two of these sites (grid squares B5 and J5) were close to the entry points for a number of rabbits who regularly frequented the fenced area, while the third site (grid square G6) was nearer to the observation hut and facilitated more accurate observations at closer range.

A simple comparison of the level of activity inside the fenced area before and during the period the golf balls were present does not reveal a clear result (Figure 13.1). Daily activity levels were variable; on days with good weather conditions and no disturbance, activity inside the fenced area ranged between 30% and 56% of transect sampling observations. Lower levels of activity were associated with a late start time for observations (October 22) and poor weather conditions (October 24 and 26). Activity inside the fenced area on the first day of the golf ball experiment was considerably higher than expected. However, weather conditions on October 28 were very favourable in marked contrast to several previous days which were cold and extremely windy. Many of the rabbits observed inside the fence line were in the northern part of the area where there were no golf balls.

When the comparison is restricted to the area around the golf balls or to grid squares B5, G6, and J5 only, a noticeable change in activity levels is evident. Substantial decreases in activity occurred within two of the grids (G6 and J5) while there was virtually no change in the third grid (B5). The overall decrease in the level of activity for all three grids combined was about 50%.

Location data from transect sampling observations were examined for all marked rabbits who frequented the areas around grid squares B5, G6, and J5. These rabbits comprised two groups: known bait-avoiders who survived the poison operation, and rabbits who never had an opportunity to encounter baits in August because their activity ranges were outside the fenced area. The presence of the golf balls caused most rabbits to avoid that part of their range with a resulting decrease in the amount of time they spent inside the fenced area (Table 13.1). Only one rabbit from each group exhibited an increase in activity inside the fenced area. Both F36 and F84 showed no adverse reaction to the golf balls.

As with the reactions to the furrow and baits during the poison operation, the responses of rabbits to the golf balls varied. Some rabbits

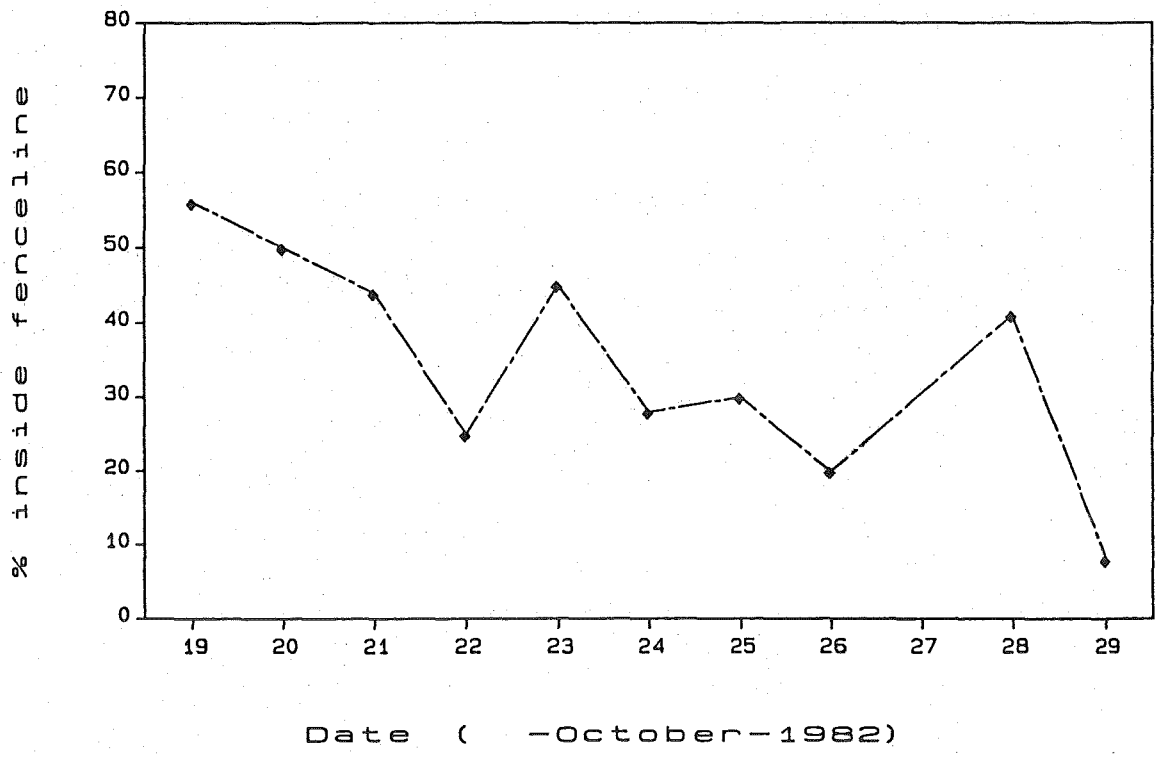


Figure 13.1 Level of rabbit activity inside the fenced area before and during the golf ball experiment.

Table 13.1 Activity levels inside the fenced area of marked rabbits before and during the golf ball experiment.

August grouping	Rabbit	Percent of transect observations Before	During
Bait avoiders:	F5	58	42
	F36	21	60
	F33	98	37
	F49	100	44
	M56	58	0
Never encountered baits:	F23	56	0
	F84	18	50
	F87	84	54
	M26	14	0
	M79	10	0
	M41	74	0

simply avoided the grid or the area near where the golf balls were located, whereas other rabbits avoided the area inside the fence line completely. Several rabbits who usually entered the fenced area through smeuse trap no.10 changed their site of entry to one of several nearby traps in order to avoid close contact with the golf balls located in grid square J5. Although M41 was twice observed entering the area through trap no.10, he ran from the area on both occasions after a quick inspection of the golf balls. Apart from F36, F84, and two unmarked individuals, no other rabbits were observed closer than about 3-4 m from the golf balls.

13.3 Discussion

Natural selection requires that for an ESS to persist, it must confer a benefit in either fertility or survival on those individuals which possess it (Krebs and Davies 1981). Obviously, the selection pressure for neophobic behaviour in rabbit populations subjected to regular control operations is considerable. It can safely be assumed that the majority of rabbits surviving poison operations possess this behavioural trait.

Based on the proportion of bait-takers in the population during August, the number of rabbits that did not display some form of neophobic behaviour towards the golf balls was lower than expected. However, spring growth had resulted in an increase in the amount of palatable vegetation on the study area. Combined with the lower population density following the poison operation, this reduced the nutritional stimulus for rabbits to forage inside the fenced area. Hence, the presence of unfamiliar objects in the rabbits' activity ranges was likely to have a greater effect than during August when the amount of palatable vegetation was markedly less. This suggests that the form or extent of an individual's neophobic response depends on an interaction between genotype and environment. The considerable variability of reactions during each of the neophobia experiments supports this view. Therefore, it appears that neophobia in rabbit populations does not conform exactly to Krebs and Davies (1981) definition of an ESS.

14 INTRODUCTION TO THE AUTOPSY SECTION

In addition to behavioural characteristics, other features of rabbit biology are pertinent to control operations. The success of poison operations and the potential of the surviving population for resurgence are influenced by factors such as the population's age structure and reproductive characteristics, and the condition of individuals within the population. The relevance of these factors is discussed in more detail in the introductions to the following chapters.

Information on these aspects of rabbit biology was collected from autopsies of rabbits killed during normal control operations carried out by the Alexandra Pest Destruction Board (see Table 14.1). Collections covered the period of the field work and several months afterwards. Two isolated autopsy samples were also obtained in 1983 but as these were not continuous with the main period of collection, less significance is attached to their results and they are omitted from some analyses.

Table 14.1 Number of rabbits autopsied each month and the control technique used to obtain autopsy samples.

Month	1980	1981	1982	1983
January	–	86[a]	50[a]	96[a]
February	–	109[a]	100[a]	–
March	–	101[d]	181[d]	125[a]
April	–	100[d]	93[d]	–
May	–	174[d]	92[a]	–
June	–	98[a]	144[c]	–
July	–	124[a,b]	163[a,c]	172[c,d]
August	–	214[c]	100[c]	–
September	–	111[a,c]	121[a]	–
October	33[a]	51[a]	87[a]	–
November	99[a]	152[a,b]	24[a]	–
December	76[a]	150[a,b]	106[a]	–

[a] = night-shot, [b] = day-shot, [c] = 1080 carrot, [d] = 1080 oats

As most of the information derived from autopsies involved measurement of material that had been stored in 10% formalin, an examination of this technique was essential. One set of material was weighed fresh, placed in formalin, and then reweighed after various lengths of storage in formalin. The results of this examination have been published (Fraser 1985) and are included as Appendix 3. Storage in formalin results in changes in weight and volume which vary according to the material, the quantity and concentration of formalin used, and the length of storage.

Laboratory measurement of the monthly autopsy samples occurred 2-3 weeks following collection. Therefore, information on the weight changes after 16 days storage (see Appendix 3) is relevant to some of the data presented in the following chapters. Although all the material stored showed some change from the initial fresh weight, the average difference for the left and right organs or perirenal fat after 16 days in formalin was of the order of 5% or less. Therefore, except for the liver which exhibited almost a 10% decrease in weight after 16 days, correction factors have not been applied as the weight changes were considered insignificant. Liver weights were multiplied by a correction factor of 1.103 to give values closer to the fresh weight.

It has been necessary to partition the data in several ways during analyses. Most results are presented so that individuals are grouped according to sex or age class. However, for simplicity a general criterion of age was sometimes more convenient; rabbits were classified into either young or adult classes with nine months used as the separation point. This is compatible with many earlier rabbit studies in New Zealand (e.g. Watson 1957, McIlwaine 1962, Wodzicki and Darwin 1962) which were carried out before accurate ageing techniques were available. Division into age classes in these studies was based on epiphyseal fusion of the tibia (Watson and Tyndale-Biscoe 1953) and the lumbar vertebrae (Taylor 1959). Such techniques could not distinguish between rabbits less than $9\frac{1}{2}$ months old, although above this age three distinct age categories were recognisable.

15 AGE AND SEX STRUCTURE

15.1 Introduction

Information on the age and sex structure of populations is of fundamental importance in the investigation and management of those populations. An understanding of the dynamics of rabbit populations can provide an insight into what regulating factors are important. Numerous irruptions and crashes of rabbit populations have occurred in the past (see Wodzicki 1950). However, most parts of New Zealand now contain stable, low density populations that pose no threat to agricultural production (Gibb et al. 1969, Williams 1983). Central Otago is an exception with relatively high rabbit densities over much of the region. The age and sex structure of Central Otago rabbit populations in comparison with low density populations elsewhere is therefore of considerable interest.

Most studies involving the analysis of population dynamics or physiological parameters require an assessment of age. An important feature of such studies is often the nature of age-related differences and to a large extent the reliability of this information depends on the accuracy of the ageing technique. As the principal method of age determination used in most recent studies was developed for rabbit populations in Australia, an assessment of its suitability for ageing New Zealand rabbits would be very useful. The availability of a small number of known age rabbits from a natural population allowed a limited assessment of the ageing method.

Rabbits often exhaust their food supplies and undergo rapid and prolonged declines in population size (Myers 1971, Gibb et al. 1978). Behavioural mechanisms of population regulation recorded for many birds and other mammals (Chitty 1960, 1967, Wynne-Edwards 1962, Christian and Davis 1964) do not appear to operate for rabbits; instead, rabbit populations are usually limited by their mortality rate. Increases in population density can cause reductions in fecundity (Mykytowycz 1960, Myers and Poole 1962, 1963) and changes in

social behaviour (Myers and Poole 1963, Myers 1968) but these factors appear to play no part in the regulation of rabbit numbers. Even when such factors are operating, rabbits reproduce at a rate considerably greater than that required for replacement. Most rabbit populations in their introduced range are limited by density-dependent interactions with their food supply, often compounded with the effects of predators and disease (Myers 1971, Gibb 1981).

The apparent lack of any self-regulating mechanism may be an indication of the rabbit's evolutionary history; in its original environment predation is the key mortality factor (Jaksic and Soriguer 1981, Soriguer and Rogers 1981). In mediterranean Spain the rabbit is an important prey item for more than 40 species of vertebrates (mainly birds of prey), many of which depend on the rabbit for the bulk of their food supply (Delibes and Hiraldo 1981). The rabbit's high reproductive rate (see chapter 17) has probably evolved partly as a response to the high level of predation pressure. It is little wonder that its translocation from a system in ecological balance to favourable habitats with many fewer predators has resulted in dramatic population explosions. Considering the lack of intrinsic density-related mortality factors, information on mortality patterns may provide some indication of what factors exert a regulating influence on rabbit populations in Central Otago.

Mortality sometimes operates unevenly on males and females (Hanson 1963, Myers 1978, Anderson and Barrett 1982) thereby unbalancing the sex ratio. Variation in the sex ratio can also occur as a result of reproductive strategies, where investment in one sex is favoured because of differential survival in resource-limited situations (Trivers and Willard 1973, Oksanen 1981). Therefore, examination of the sex ratio may provide additional information on the rabbit's relationship with the environment in Central Otago.

15.2 Results and Discussion

15.2.1 Ageing technique

The technique most commonly used for ageing rabbits in population studies is that based on the dried weight of the crystalline eye lens. This method was originally devised by Lord (1959) for cottontail rabbits and subsequently developed for the European rabbit in Australia by Dudzinski and Mykytowycz (1961) and Myers and Gilbert (1968). Age is calculated according to the formula:

$$\text{age (days)} = -57 + 181.4 \,/\, \ln \frac{314}{\text{lens wt. (mg)}}$$

with a standard deviation of about 11% (Myers and Gilbert 1968). The formula is derived from a composite growth curve using data from a range of environments. This method is reasonably accurate for determining the age of rabbits up to 24 months old, but thereafter the possible error is large and no differentiation should be made on the basis of eye lens weight for rabbits in the asymptotic region (i.e. >24 months).

Lord (1959) and Myers and Gilbert (1968) demonstrated that the growth of the eye lens is relatively insensitive to environmental variation in comparison with other body measurements. In Australia regional variation in the growth rate of the eye lens has been recorded (Myers and Gilbert 1968, Wheeler and King 1980) but differences are relatively minor and do not markedly affect general age structure results. Regional differences may be due to several factors including genetic variation (Rongstad 1966), nutritional factors (Lord 1959), and age-related mortality (Connolly et al. 1969).

Differentiation of rabbits older than 24 months into yearly age classes is possible based on counting the adhesion lines in the periosteal zone of the lower mandible (Henderson and Bowen 1979). Similar methods are used for age determination in a variety of mammals (see Klevezal and Kleinenberg 1967, Morris 1972) although they are best suited to species with an average life

span of several years. Nevertheless, adhesion lines have been used to determine age in some lagomorphs (Sullins et al. 1976, Frylestam and Von Schantz 1977).

The other major ageing technique commonly used in rabbit studies is based on skeletal criteria. Rabbits may be classified into four age classes (<10 months, 10–25 months, 26–33 months, and >33 months) depending on the degree of epiphyseal fusion of the tibia and the lumbar vertebrae (Watson and Tyndale-Biscoe 1953, Taylor 1959). Some differentiation among rabbits in the youngest age class is possible. Wodzicki and Darwin (1962) determined the age of rabbits less than three months old according to Whittle's (1955) modified curve showing the relationship of paunched weight to age. Gibb et al. (in press) aged rabbits up to five months old from the length of the tibia, excluding both epiphyses.

The quantity of material examined during this study and the more detailed results required favoured the eye lens technique. In addition, it was already known that most Central Otago rabbit populations contain relatively few rabbits greater than 24 months old (J Bell pers. comm.) so determining the exact age of rabbits greater than 24 months old was not critical. The eye lens technique was also preferred because it is a quantitative measurement rather than a subjective classification of age. Despite reference to known age material, observer bias can lead to considerable discrepancies in age distributions based on epiphyseal fusion (Gibb et al. in press).

Eye lens weights from a small number of rabbits of known age that were killed during the Butchers Dam poison operation allowed the suitability of Myers and Gilbert's (1968) ageing formula to be checked. Table 15.1 gives details of marked rabbits killed during the poison operation. The season of birth refers to the most recent possible breeding season in which an individual could have been born; in some cases rabbits may have been born earlier. Although not marked until July 1982, F177 who had distinctive patches of white fur was first observed on the study area in November 1980 as an adult

Table 15.1 Capture weight, approximate birth date, and age, compared with age according to eye lens weight for rabbits killed during the Butchers Dam poison operation, August 1982.

Rabbit	Date of capture	Capture wt. (g)	Approx. birth date	Approx. age (weeks)	Eye lens wt. (mg)	Age (weeks)
M23	Jan 1981	1700	1979/80	–	279	>104
M37	May 1981	1150	Jan 1981	81–85	239	87
M46	Sep 1981	1450	1980/81	–	238	85
M47	Oct 1981	1650	1980/81	–	257	>104
M64	Jan 1982	1100	Oct 1981	42–46	190	43
M71	Feb 1982	1600	1980/81	–	239	87
M78	Jul 1982	1550	1981/82	–	237	84
F24	Jan 1981	900	Oct 1980	94–98	244	95
F41	Feb 1981	1150	Sep 1980	98–102	255	>104
F42	Feb 1981	1500	1979/80	–	252	>104
F52	Jul 1981	1500	1980/81	–	237	84
F61	Nov 1981	1550	1980/81	–	276	>104
F66	Dec 1981	850	Sep 1981	46–50	200	49
F69	Dec 1981	1550	1980/81	–	235	81
F177	Jul 1982	1650	1979/80	–	258	>104

rabbit. Therefore, F177 was born in the 1979/80 breeding season or earlier.

In all cases the age determined using eye lens weight was confirmed by the approximate date of birth calculated from initial capture weight. In most cases weight data could not be used to define date of birth more accurately than the overall breeding season. However, for those rabbits first captured below the asymptotic weight range (M37, M64, F24, F41, and F66) a much closer estimate of the date of birth could be made. During the first few months, weight increase is essentially linear (see section 16.2.1, also Southern 1940, Dunnet 1956) and approximate birth dates can be calculated to the nearest month from capture weight information. With the exception of M37 and F41, both methods ascribed date of birth to the same month. For M37 and F41 the date of birth estimates vary by about one month, although in the case of F41 it is difficult to be precise because eye lens weight is close to the range where it is unreliable.

Overall, it appears that results obtained using the ageing formula developed for rabbits in Australia fall within acceptable limits for a general classification of age structure. Because of the age structure of Central Otago rabbit populations (see section 15.2.2) the scope for error is small. In addition, possible variation in eye lens growth rates between Australian and Central Otago rabbits would not affect inter-population comparisons within Central Otago. Where extremely accurate ageing is necessary, Wheeler and King (1980) recommend that regional eye lens growth curves be determined. These require an assumption that the environment of the known age rabbits is representative of the area being sampled. While such accuracy is desirable for detailed studies, the use of a composite growth curve formula is preferable if comparisons are being made between a number of different areas.

15.2.2 Age structure

The overall age distribution for all rabbits collected during the study reveals the considerable sampling bias associated with shot or poisoned samples (Figure 15.1). Rabbits less than six months old are grossly under represented; the small proportion of rabbits in the 0-3 month age range is particularly noticeable. This problem is common in rabbit population studies, particularly for samples collected by shooting (Myers 1971, Williams and Robson 1985, Gibb et al. in press). Behaviour differences between rabbits less than six months old and older rabbits probably account for this sampling bias. Young rabbits move over smaller distances (Daly 1979, Parer 1982) and display more alert behaviour (see Section 6.2.6) than older rabbits. Therefore, they are probably less susceptible to sampling by control methods than older rabbits.

Age distributions for individual months were broadly similar to this basic pattern although there were obvious fluctuations according to the time of year (Figure 15.2). Predictably the proportion of young rabbits was greatest in samples collected during and immediately following the breeding

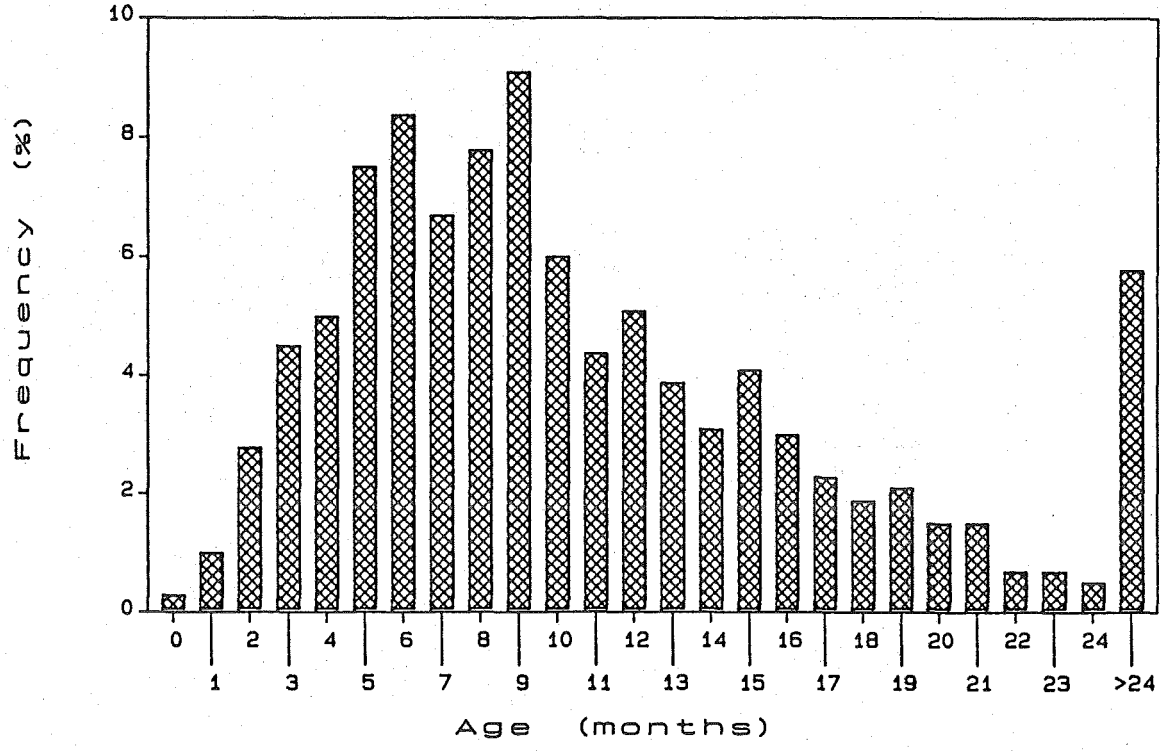


Figure 15.1 Age distribution of approximately 3300 rabbits collected for autopsy between October 1980 and July 1983.

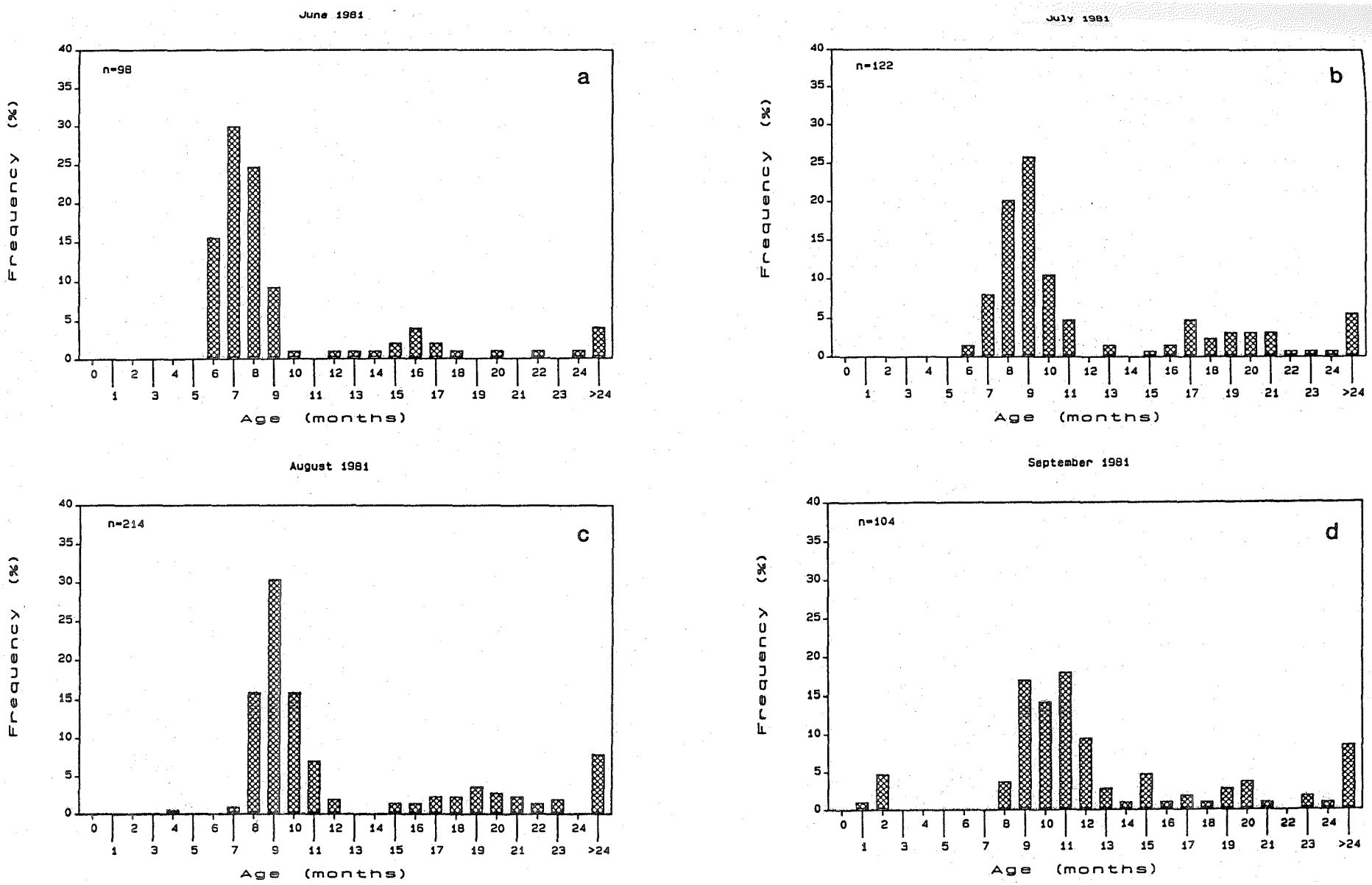
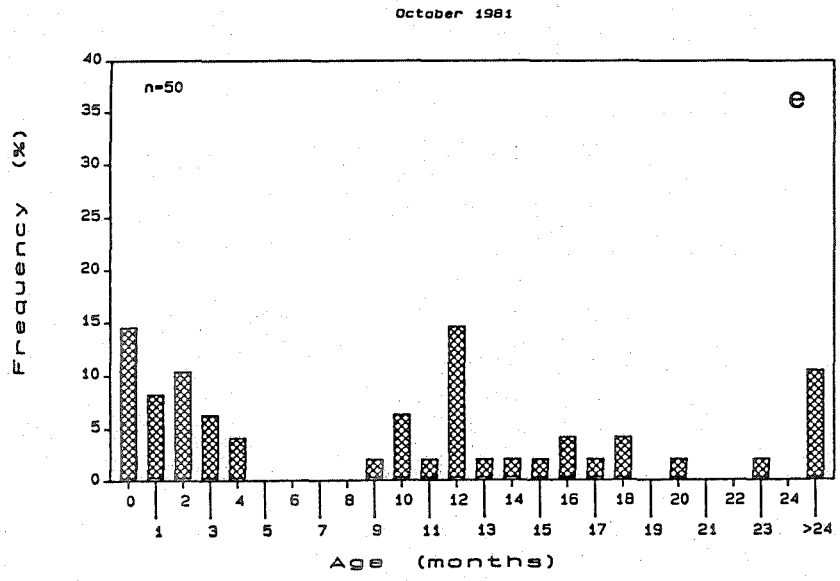
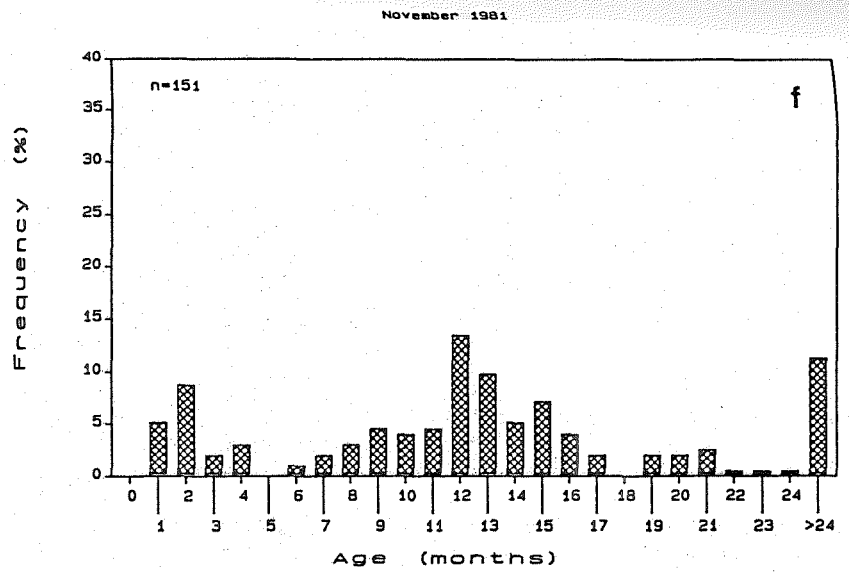
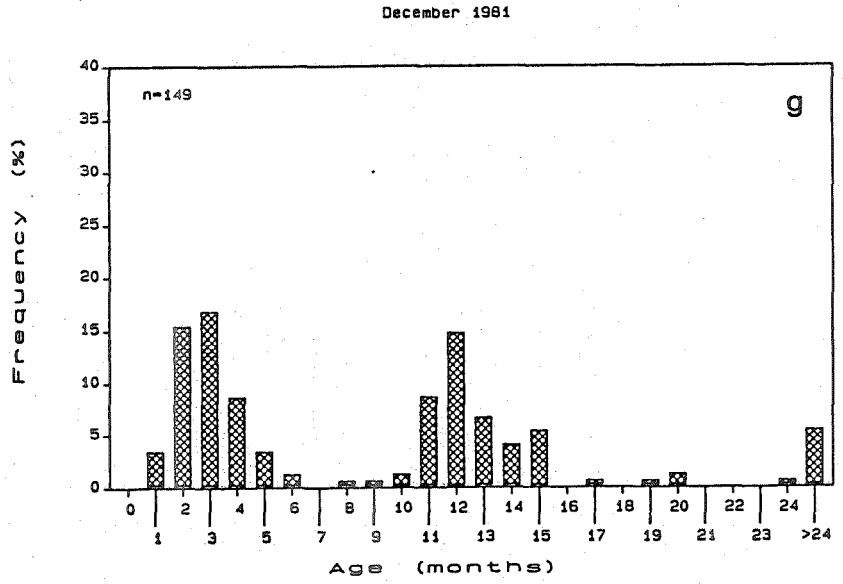
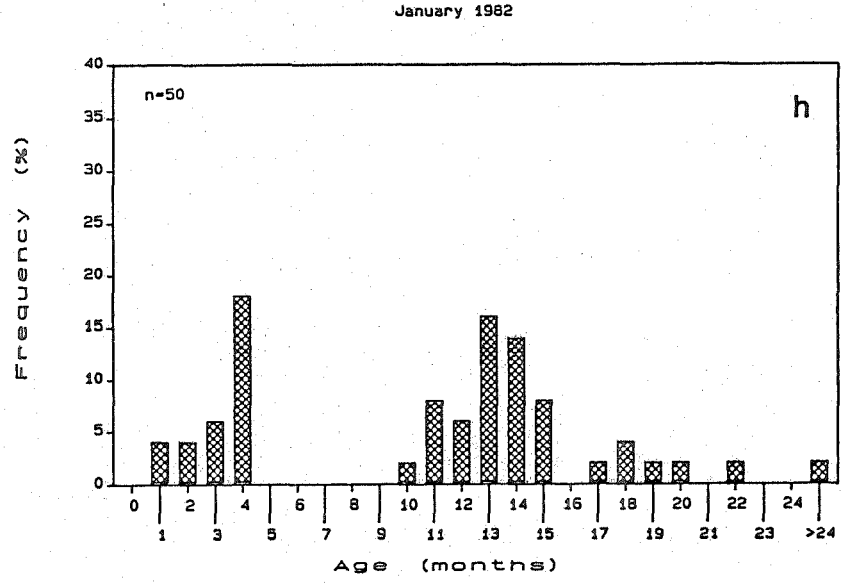


Figure 15.2 (a-l) Age distributions for each month's autopsy sample between June 1981 and May 1982.

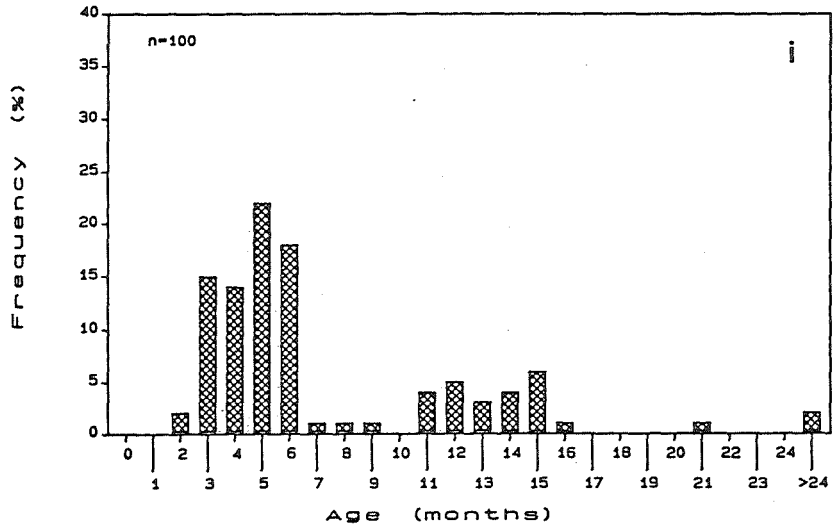

October 1981
n=50
e
Frequency (%)
Age (months)


November 1981
n=151
f
Frequency (%)
Age (months)


December 1981
n=149
g
Frequency (%)
Age (months)


January 1982
n=50
h
Frequency (%)
Age (months)

February 1982



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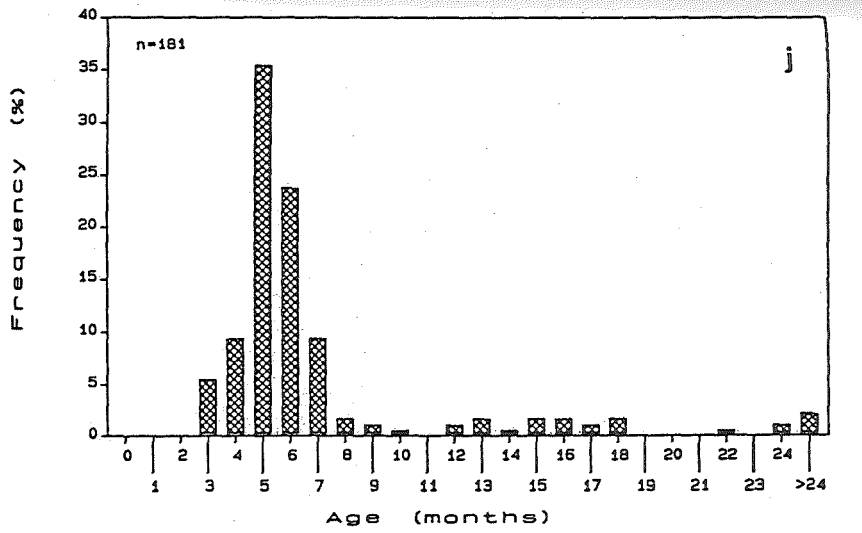

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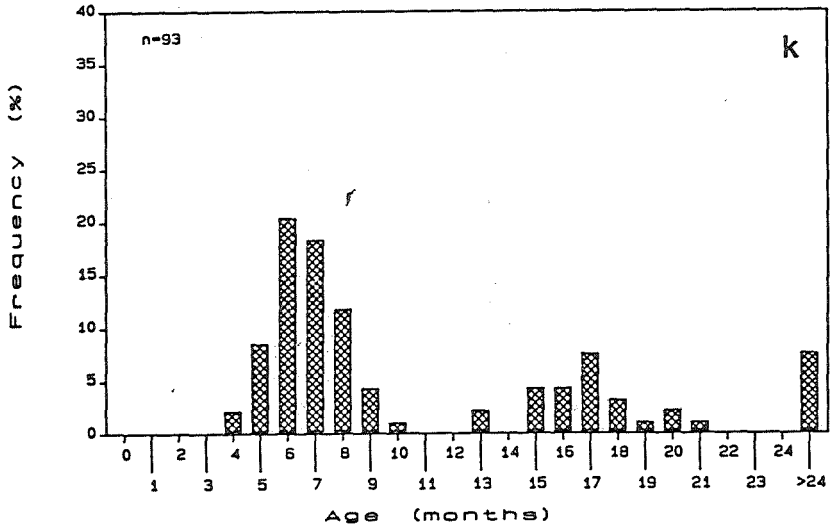

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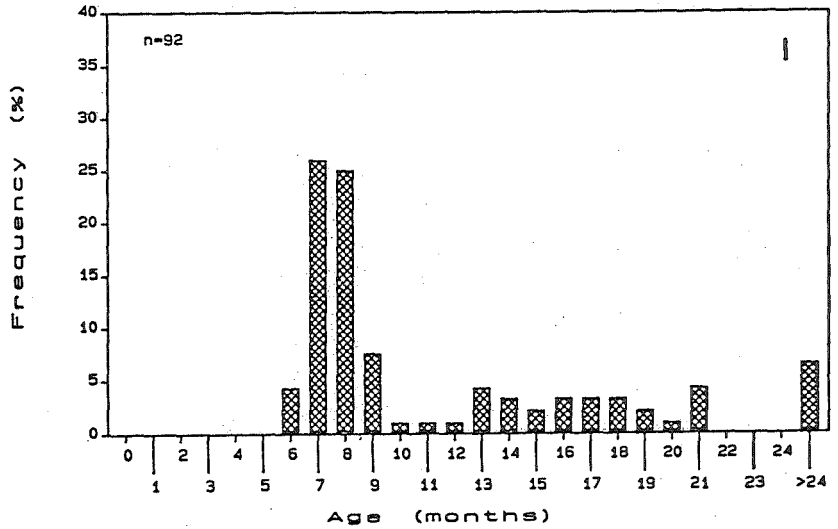

season. Each breeding season's birth pulse formed a peak within the age distribution which appeared at successively greater ages for consecutive months. The peak frequencies for rabbits between 12 and 24 months old were generally much lower than for rabbits less than 12 months old, indicating a high mortality rate (see section 15.2.3).

The age structures exhibited by rabbit populations in Central Otago differ from populations in other parts of New Zealand mainly in the proportion of rabbits greater than 24 months old. This category comprised about 6% of all rabbits sampled (range of monthly samples: 2-12.5%) compared with almost 20% for rabbit populations in the Wanganui region (Williams and Robson 1985) and 15% in the Wairarapa area (Gibb et al. in press). The overall age distribution for Central Otago rabbit populations is almost identical to that for populations in subalpine New South Wales (Myers 1971). Age distributions with large numbers of young rabbits and very few older individuals suggest high mortality and a rapid turnover rate.

The median age was 9.4 months for males and 8.8 months for females. A true mean age could not be calculated as all rabbits greater than 24 months old were automatically grouped into an arbitrary age class. However, as the proportion in this class was small it would not be expected to significantly increase the calculated mean ages of 10.9 months for males and 10.3 months for females (when this class was ascribed the arbitrary age of 25 months). The number of rabbits which reach ages of 36 months or more is probably very small. Some evidence for this can be inferred from the age distributions in Figure 15.2. The highest proportions in the >24 month category (August-November 1981) occur close to the peak of reproductive activity when rabbits in this category are likely to be only just greater than 24 months old. These rabbits represent the progeny of the breeding season two years previous. The decrease in the proportion of rabbits in this category during subsequent months indicates that probably 2% or less of rabbits over about six months old reach an age of 36 months.

15.2.3 Mortality

A prerequisite for the analysis of mortality rates is the assumption that a population has a stationary age distribution; the population must have a zero rate of increase and a stable age structure (Caughley 1977). Comparison of the age structure of populations sampled throughout the study does not reveal any significant differences in population trends. Small fluctuations in population size (and hence rate of increase) do not greatly affect mortality rates provided the fluctuations have a mean wave length considerably shorter than the period over which the samples are collected (Caughley 1967). The relative stability of the environment in Central Otago and the predictability of weather conditions suggest that marked fluctuations in population size are unlikely. Spotlight counts of rabbits on the Butchers Dam area by Rabbit Research Group (MAF) over several years (Figure 15.3) confirms this assumption (W D Ross pers. comm.). On this basis a crude life table analysis is justified.

The considerable sampling bias resulting in low numbers of young rabbits precludes a strict analysis of mortality from birth. Instead, mortality rates were calculated for rabbits greater than six months old, with the data partitioned into 3-month age classes. (Table 15.2). Because of the inability to classify rabbits greater than 24 months old into 3-month age classes, mortality rates cannot be calculated for rabbits in this category.

Mortality was relatively uniform for rabbits aged between 6 and 21 months but considerably higher for the 21-24 month age class. Rabbits in this age class are generally entering their second breeding season and the additional physiological stress of reproductive activity may be a cause of increased mortality. Mortality rates for rabbits up to six months and greater than 24 months old can only be speculated on, although evidence from previous studies provides an indication of general trends. Mortality is very high in young rabbits up to three months old (Southern 1940, Tyndale-Biscoe and Williams 1955, Myers 1971, Martin 1977). Most of this mortality probably occurs at the

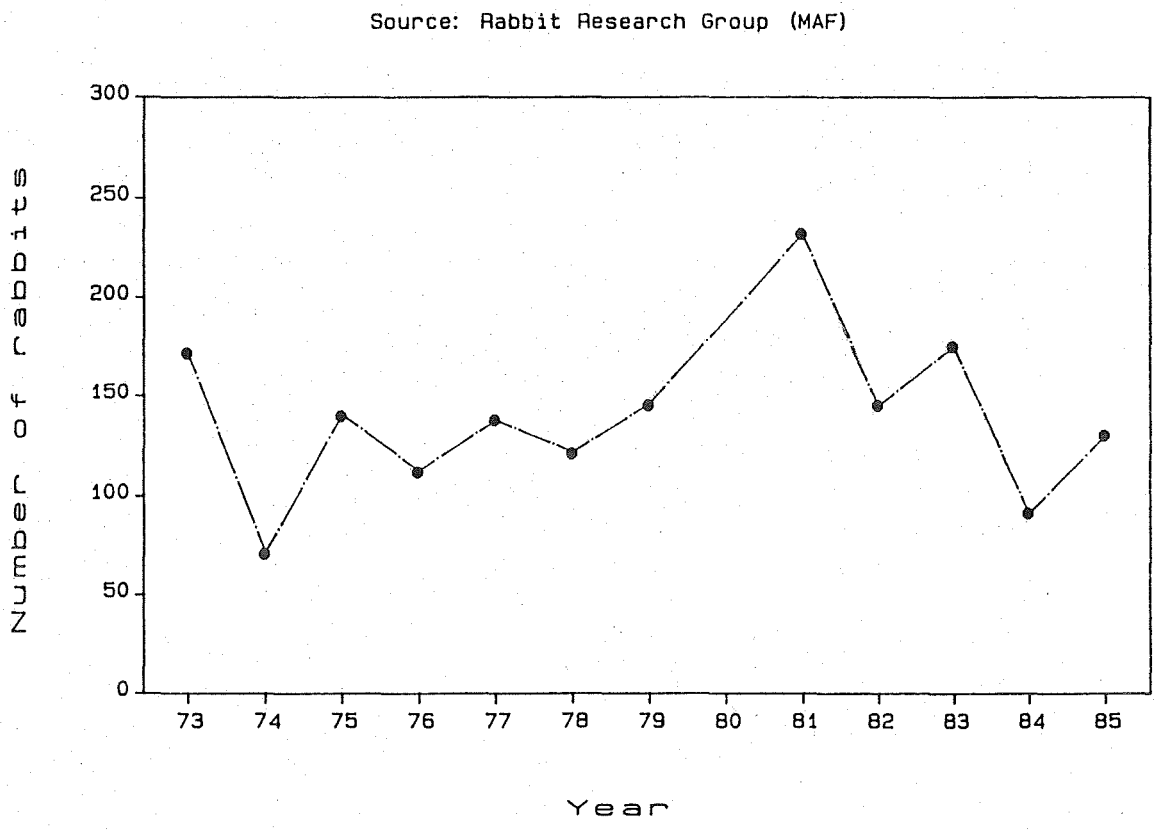

Figure 15.3 Spotlight count results for a fixed route on the Butchers Dam research area during winter months.

Table 15.2 Life table analysis* for all rabbits collected for autopsy.

Age class (months) x	Frequency fx	Survival lx	Mortality dx	Mortality rate qx
0–3	281			
4–6	696			
7–9	787	1.000	0.346	0.346
10–12	515	0.654	0.183	0.280
13–15	371	0.471	0.161	0.342
16–18	244	0.310	0.095	0.306
19–21	169	0.215	0.131	0.609
22–24	66	0.084		
>24	195			

* for definition of terms, see Caughley 1977, p.86

nestling stage when young rabbits are susceptible to a range of mortality factors including cold weather, flooding of breeding stops, disease, predation, and starvation. Indirect evidence for the high level of mortality operating on nestling rabbits was obtained during behaviour observations on the Butchers Dam study population. The most frequently observed number of recently emerged young from the same litter was three, compared with the average litter size at parturition of 6.07 for rabbits in Central Otago (see section 17.2.5).

It appears that those rabbits that reach an age of three months have a good chance of surviving to adult age classes. However, results presented by Tyndale-Biscoe and Williams (1955) suggest that these rabbits probably constitute less than 20% of those born. The mortality rate is still relatively high for rabbits greater than six months old and most rabbits survive only for one breeding season. The low level of fat reserves in rabbits less than six months old (see section 16.2.2) may help to explain why juvenile mortality is high. Severe weather conditions during late autumn and winter combined with the poor food supply during this period may cause heavy mortality, both directly through starvation or indirectly through reduced resistance to

disease and parasites (Bull 1953a, 1957, Tyndale-Biscoe and Williams 1955) or increased vulnerability to predators (Gibb et al. 1978). High mortality is a characteristic of many rabbit populations (e.g. Southern 1940, Tyndale-Biscoe and Williams 1955, Martin 1977). Myers (1971) suggests that survival rates increase markedly for rabbits greater than 24 months old in arid and mediterranean regions of New South Wales. However, Myers did not demonstrate stability for the populations he studied so his life table analysis may be invalid.

Following the increased mortality associated with the second breeding season (mortality rate of 0.609 between the 18-21 and the 21-24 month age classes) it is probable that adult survival improves as indicated by the actual number of rabbits in the >24 age class. Trial-and-error calculations reveal that an average 3-month mortality rate of 0.324 results in about 2% of rabbits surviving to an age of 36 months (as suggested in section 15.2.2). Therefore, it appears that the mortality rate of adult rabbits is approximately 0.3 per 3-month period, a similar rate to that found for rabbits in Hawke's Bay (Tyndale-Biscoe and Williams 1955). During the second and possibly subsequent breeding seasons adult mortality increases considerably although the effect of physiological stress due to reproductive activity is not evident for rabbits in their first breeding season.

In comparison with other parts of New Zealand where productivity is higher (see section 17.2.5), rabbit survival must be considerably greater in Central Otago to account for the higher population densities. Considering the similarity of adult mortality rates between Central Otago and a low density population in Hawke's Bay (Tyndale-Biscoe and Williams 1955), variation in juvenile mortality must account for these differences. Juvenile mortality due to parasites and disease is considerable in areas of higher rainfall (Bull 1953a, Tyndale-Biscoe and Williams 1955) but may be insignificant in Central Otago where rainfall is very low and conditions for juvenile survival are markedly better.

The basic mortality trends observed for rabbits in Central Otago and in previous studies conforms to the typical mammalian pattern (Caughley 1977) although a steady increase in adult mortality is not evident in most studies. There is evidence to support this feature from other lagomorphs (Kovacs 1983). Juvenile mortality rates vary considerably between populations (Myers 1971) whereas adult mortality rates are less variable. When such conditions exist, fluctuations in juvenile mortality are most likely to be responsible for fluctuations in rate of increase. Therefore, because of the relative stability and predictability of environmental conditions in Central Otago compared with other areas of favourable rabbit habitat in New Zealand, rabbit populations in Central Otago are probably less likely to fluctuate widely even though they remain at high densities.

15.2.4 Sex ratios

Monthly samples exhibited no significant differences from parity in the sex ratio (Table 15.3). However, a definite trend in favour of males was evident in most (22 of 30) samples. Overall, males comprised 51.7% of the total number of rabbits collected (chi-square=3.70, p=0.054). The heterogeneity chi-square (Zar 1974) confirms that the monthly samples are homogeneous and may be pooled for further analysis.

Discrepancies in the sex ratio became apparent when the data were examined according to 3-month age classes (Table 15.4, Figure 15.4). Females predominate in the 0-3 and 4-6 month age classes, but thereafter the number of males in each age class exceeds that of females. Assuming a 50:50 sex ratio at parturition (Brambell 1944, Mills 1955, Boyd 1985), young male rabbits either suffer higher mortality during their first few months or are less susceptible to sampling by control methods than young females. Behaviour differences may cause a sampling bias but higher mortality among males is more likely. Young males suffer more aggression from adult rabbits (Mykytowycz 1959, 1960, Myers and Schneider 1964) and are therefore more likely to disperse (see section

Table 15.3 Sex ratios of monthly autopsy samples.

Month	Males	Females	Chi-square	Significance
October 1980	16	17	0.00	-
November	50	49	0.00	-
December	45	31	2.22	0.14
January 1981	39	47	0.57	0.45
February	55	54	0.00	-
March	50	51	0.00	-
April	42	58	2.25	0.13
May	81	93	0.70	0.40
June	49	49	0.00	-
July	71	52	2.33	0.13
August	111	103	0.23	0.63
September	51	60	0.58	0.45
October	23	28	0.31	0.58
November	75	75	0.00	-
December	83	67	1.50	0.22
January 1982	29	21	0.98	0.32
February	53	47	0.25	0.62
March	92	89	0.02	-
April	46	47	0.00	-
May	52	40	1.32	0.25
June	79	65	1.17	0.28
July	82	81	0.00	-
August	56	44	0.91	0.34
September	61	60	0.00	-
October	44	43	0.00	-
November	15	9	1.04	0.34
December	62	44	2.73	0.10
January 1983	53	43	0.84	0.36
March	64	61	0.03	0.86
July	93	79	0.98	0.32
Total of chi-squares			20.96	p>0.80
Total	1722	1610	3.70	0.054
Heterogeneity chi-square			17.26	p>0.95

8.2.6). Consequently, young males are probably more susceptible to predation and other mortality factors during their first few months, leading to a disparate sex ratio in favour of females.

The shift in the sex ratio in favour of males occurs at an age class (10-12 months) where most female rabbits are beginning to breed for the first time. The additional stresses imposed by reproduction probably contribute to higher mortality among females around this age. The difference is probably

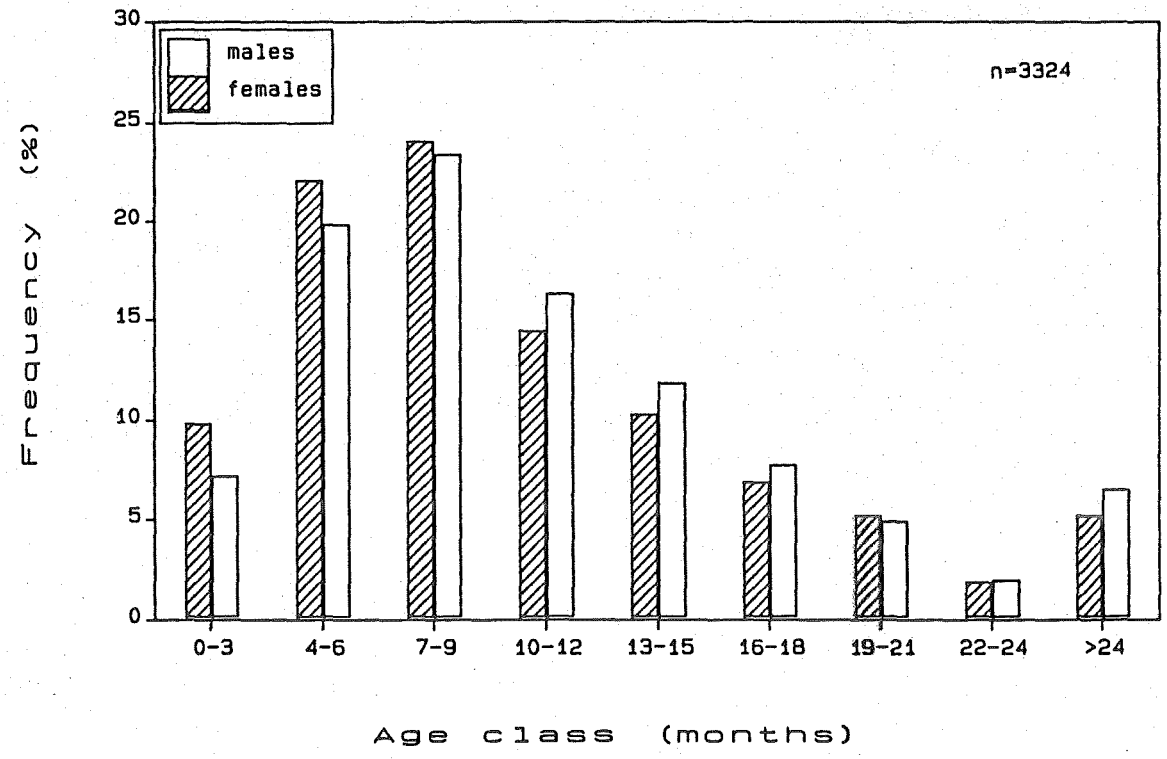

Figure 15.4 Age class distributions for the male and female segments of the population (all autopsy data pooled).

Table 15.4 Variation in sex ratio according to age class.

Age class (months)	Males n	Males %	Females n	Females %	Chi-square	Sign.
0- 3	124	7.2	157	9.8	3.64	.056
4- 6	341	19.8	355	22.1	0.24	.62
7- 9	402	23.4	385	24.0	0.33	.57
10-12	282	16.4	233	14.5	4.47	.034
13-15	205	11.9	166	10.3	3.89	.048
16-18	133	7.7	111	6.9	1.81	.18
19-21	85	4.9	84	5.2	0.00	-
22-24	35	2.0	31	1.9	0.14	.71
>24	112	6.5	83	5.2	4.02	.045

exaggerated by variation in behaviour between males and females at this age. Greater activity by males would make them more susceptible to sampling. A significant difference in favour of males in the >24 month age class has also been recorded by Williams and Robson (1985) and Gibb et al. (in press).

Age-related variation in the sex ratio is by no means similar in all populations. Myers (1971) recorded higher survival for adult females in mediterranean New South Wales, but this trend was reversed in arid New South Wales. Rogers (1979) also found a predominance of females in older age classes and suggests that this may be caused by increased predation of males because of their greater activity and home range size. Because of these differences it is unclear whether differential mortality occurs for males and females or whether sex ratio differences are due to sampling biases. When food resources are limiting, as they commonly are during late autumn and winter months in Central Otago, density-dependent mortality would be expected to be greater for males. Higher survival of females is a useful evolutionary strategy which minimises the loss of reproductive potential of the population during times of hardship. This mechanism does not appear for operate in rabbit populations in Central Otago, unless its effects are masked by sampling biases or other mortality factors.

16 GROWTH AND CONDITION

16.1 Introduction

Whereas age structure gives an indication of the overall status of a population in relation to its environment, an analysis of growth and condition provides information on the state of individuals within that population. Growth rates are indicative of environmental favourability, particularly during the early stages of an animal's lifespan, and can provide an index for the comparison of populations from different environments. On the other hand, fat-related condition is a more dynamic measure and reflects an animal's responses over a shorter period to environmental conditions, especially nutritional factors (Riney 1955, Challies 1973). Fat reserves are also related to a population's rate of increase (Caughley 1967, Bamford 1972, Martin 1977). Although many other factors including physiological vigour and the incidence of disease and parasites contribute to an animal's condition, here as in many other mammal studies condition is used as a synonym for fat reserves.

As Caughley (1967) suggests, a growth curve for a single individual accurately traces its growth over a particular period but a mean growth curve for a population is little more than an abstraction. Mean growth curves are based on survivors and any variation in mortality rates can influence these curves, especially if mortality acts differentially on particular size classes (e.g. smaller individuals). Nevertheless, the information provided for length and weight changes with age are applicable to a gross comparison of rabbits from Central Otago and other areas. In addition, the relationship between an animal's weight and length can be used to assess its condition (Bamford 1970).

Riney (1955) investigated several indices of fat-related condition for red deer and concluded that an index based on the weight of perirenal fat gave the best indication of total fat reserves. The kidney fat index (KFI) is calculated as 100 times the weight of perirenal fat, divided by the weight of the kidney. Inclusion of kidney weight in the index corrects for variation in

body size and therefore allows direct comparison between rabbits of different sizes. However, when fat reserves are severely depleted the accuracy of the KFI is questionable and other indicators such as bone marrow fat may be more useful (Ransom 1965, Martin 1977). This arises because different fat reserves are mobilised sequentially (Cheatum 1949, Riney 1955, Martin 1977). Information on the sequence of fat mobilisation in possums (Bamford 1970) and rabbits (Martin 1977) indicates that abdominal fat reserves show the closest relationship to environmental conditions and changing seasonal patterns. Bamford (1970) measured mesogastric fat levels because it was difficult to define the precise limits of perirenal fat for possums.

Seasonal variation in kidney weight can distort the KFI for red deer (Batcheler and Clarke 1970) and feral sheep **Ovis aries** (Van Vuren and Coblentz 1985). However, Flux (1971) found that kidney weight in hares varied by only about 10% throughout the year and did not cause any significant differences in the pattern of the KFI. Although the seasonal deposition of fat may exhibit considerable variation between different age or sex classes within the same population (Smith 1973, Martin 1977), or show no direct correlation with the availability of food (Flux 1971, Rogers 1979), fat-related condition generally traces the physiological requirements of individual animals. Such variation may be the result of hormonal rather than environmental influences (Caughley 1970, Flux 1971). Fat-related condition has been used as a predictive indicator of control operation success for possums (Batcheler et al. 1967, Bamford and Martin 1971).

16.2 Results and Discussion

16.2.1 Total length, total weight, and carcass weight

The rapid neonatal growth rate of lagomorphs (Swihart 1984) is confirmed by data collected during this study. The length and weight of young rabbits increases rapidly during the first few months (Figure 16.1). In fact, by age

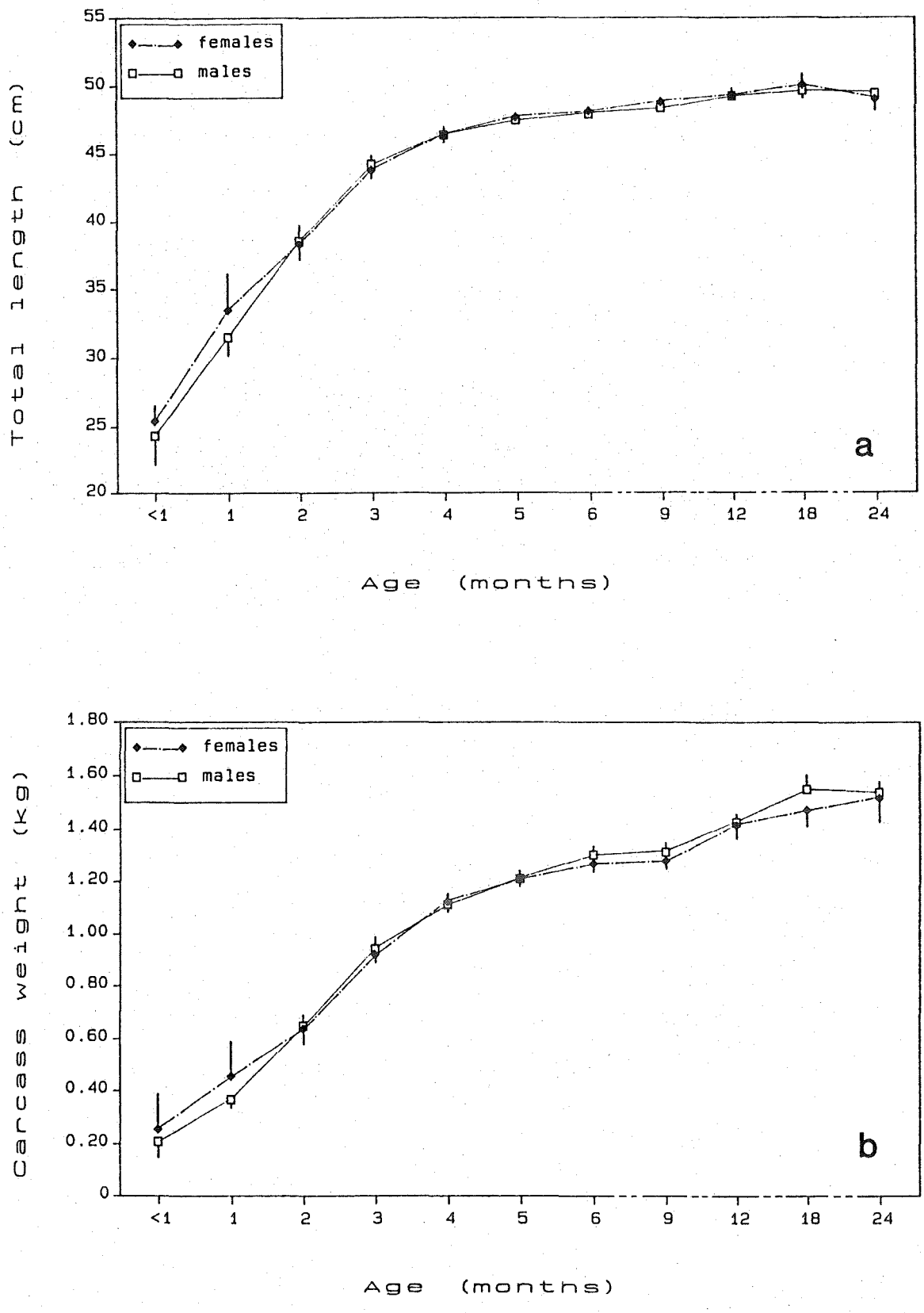

Figure 16.1 Increase in (a) total length and (b) carcass weight with age (points represent the mean together with one of the 95% confidence limits).

six months most young rabbits have attained their maximum linear dimensions, although weight continues to increase until a maximum is reached between 12 and 18 months. Between six and nine months of age no increase in weight occurs. For most young rabbits this period represents the winter months when the food supply is limited. The restricted food supply and the greater metabolic requirements for maintenance during the cold winter months restrict the opportunity for growth during this period. The subsequent resumption of increase in carcass weight coincides with the increasing availability of food during the spring months. It is interesting that many rabbits attain sexual maturity (see sections 17.2.1 and 17.2.2) before they have reached their final dimensions, a characteristic also reported for hare populations in New Zealand (Flux 1967).

The gradual increase in mean length recorded for adult rabbits over the duration of the study is puzzling (Figure 16.2). No similar trend for weight was evident (see Figure 16.4) which suggests that the pattern of increase may have been an artifact of the measuring technique. Total length was obtained by extending the rabbit on a measuring board and recording the distance from the tip of the nose to the last caudal vertebra. An increase in the holding tension applied to rabbits during measurement over the duration of the study seems the only plausible explanation for this trend. Bailey (1968) recorded considerable variation in cottontail body lengths obtained by different observers using a similar measuring technique.

Despite this apparent sampling artifact, female rabbits were consistently longer than males. Overall, this difference was significant ($t=2.27, p<.05$), and when the data are pooled by season significant differences exist for winter and spring. The greatest mean length for both sexes occurs during summer, while mean length is least during autumn months when recruitment of young rabbits into the adult age class reaches a peak (Table 16.1).

Carcass weight was chosen for comparisons in preference to total weight for a number of reasons. It exhibits less variation (CV=12.7%) than total

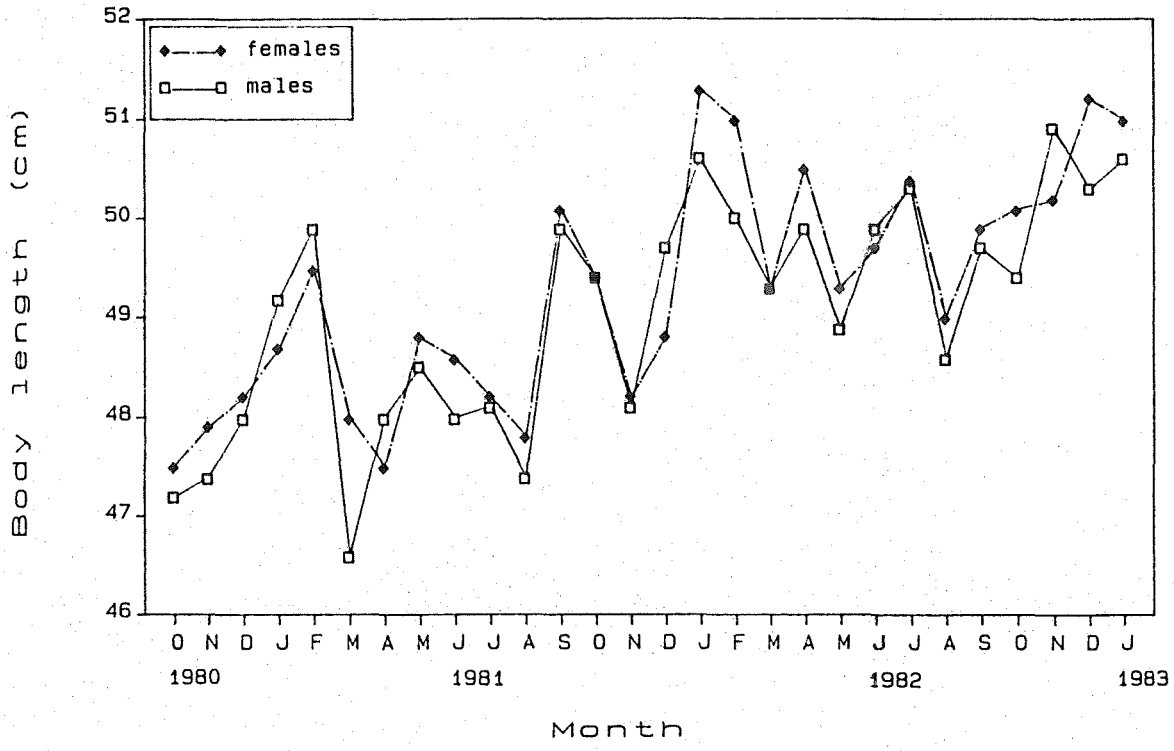

Figure 16.2 Mean body length for adult male and female rabbits.

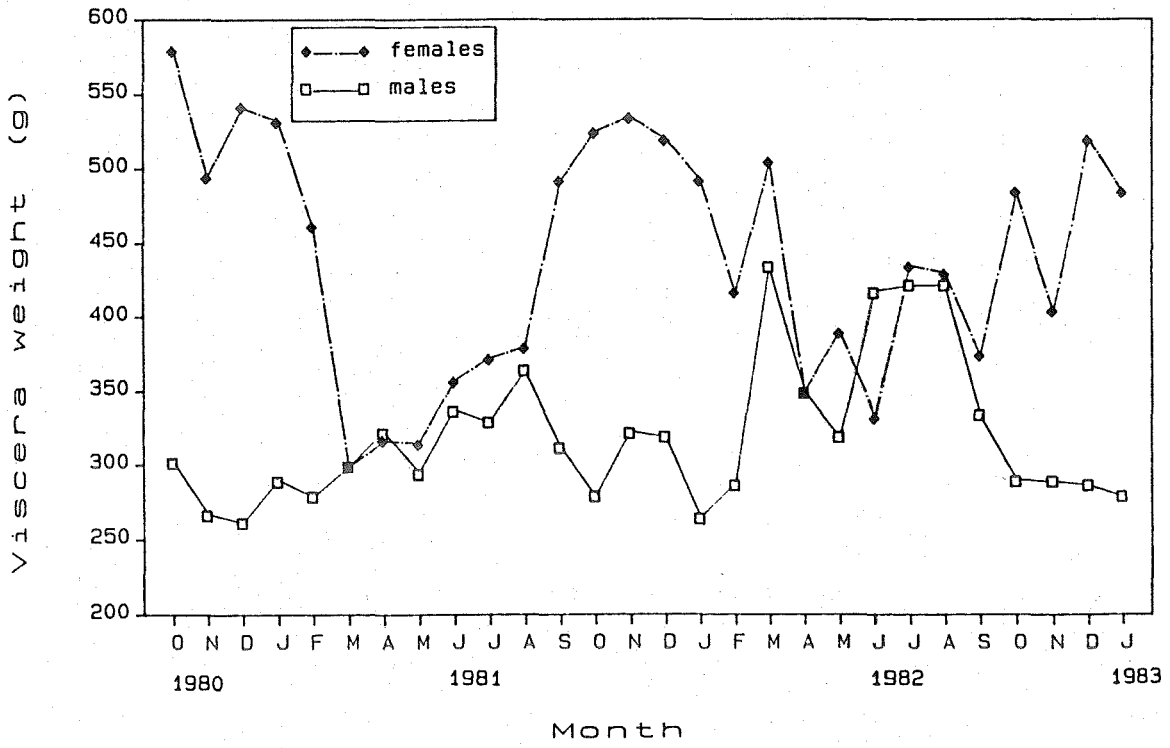

Figure 16.3 Mean weight of the viscera (and reproductive organs) for adult male and female rabbits.

Table 16.1 Mean length (cm) of adult rabbits pooled by sex and season.

Season	Males n	Males Length	Males s.e.	Females n	Females Length	Females s.e.
Summer	210	49.9	0.13	150	50.0	0.32
Autumn	132	48.8	0.19	121	49.0	0.17
Winter	342	49.1	0.11	276	49.4	0.11
Spring	282	49.0	0.12	275	49.4	0.15
Total	966	49.2	0.07	822	49.4	0.09

n = sample size, s.e. = standard error

weight (CV=14.8%) and eliminates the problem of including embryos in the total weight of pregnant females. Watson and Williams (1955) recorded considerable variation in total weights of rabbits according to the method used to obtain the sample and related this to the length of time spent feeding immediately prior to death. Stomach contents may vary from 2-9% of total weight (Watson 1954). Carcass weight was obtained after the liver, stomach and intestines, kidneys and associated fat, and reproductive organs had been removed. This differs from Watson and Williams' (1955) paunched weight in that they did not remove the kidneys and associated fat. However, the weight of this material represents only about 1.3% of the carcass weight so the difference between carcass weight and Watson and Williams' paunched weight is negligible.

An indication of the variability produced by inclusion of the viscera and reproductive organs is evident from the seasonal variation in the weight of this material for adult rabbits (Figure 16.3). Whereas viscera weight for males and females was similar during the non-breeding season, highly significant differences were associated with the incidence of pregnancy among females (ANOVA, $F=722.77$, $p<.001$). Gibb et al. (in press) report that the difference in mean total weight between males and females varies seasonally according to the proportion of females pregnant. Consequently, carcass weight was assumed to be a more reliable indicator to illustrate seasonal trends and

sexual dimorphism within the samples collected.

Carcass weight for adult male rabbits was consistently heavier than for females (Figure 16.4), except during summer months when females were slightly heavier than males. Although embryos and uteri were removed from females, the additional weight of the mammary glands at this time of the year may account for this difference. When the data were pooled by season, carcass weight differences were shown to be significant ($p<.05$) for autumn and winter only.

Rabbits in Central Otago appear to reach greater weights than found in other areas. Brambell (1944) found that for rabbits in Wales the highest frequency class for carcass weight was 1150–1200 g for both sexes and that less than 1% of rabbits sampled (n=1884) had carcass weights greater than 1500 g. Watson (1957) recorded paunched weights of 1294 g and 1305 g for adult (>9½ months) males and females respectively in Hawke's Bay. McIlwaine (1962) reported greater mean weights (1385 g for males and 1381 g for females) for rabbits collected from the same area during a later study. In comparison, mean weights for adult rabbits collected in Central Otago were 1472 g for males and 1434 g for females. The sexual dimorphism in carcass weight evident for rabbits from Central Otago ($t=3.61, p<.001$) has not been recorded in previous studies (Brambell 1944, Watson 1957, McIlwaine 1962, Andersson, Dahlback and Meurling 1979). The greater size reached by rabbits in Central Otago combined with the harsh environmental conditions for part of the year, and the greater influence of such conditions on female rabbits, may account for this difference between males and females.

Despite substantial environmental variation between areas for which data are available, size as indicated by carcass weight follows Bergmann's rule (Figure 16.5). This rule states that within a species individuals are progressively larger the further they live from the equator. This evidence conflicts with Mayr's (1963) statement that burrowing mammals do not conform to Bergmann's rule. Rabbits from northern hemisphere populations appear to be smaller overall, and the relationship between size and latitude is clearer

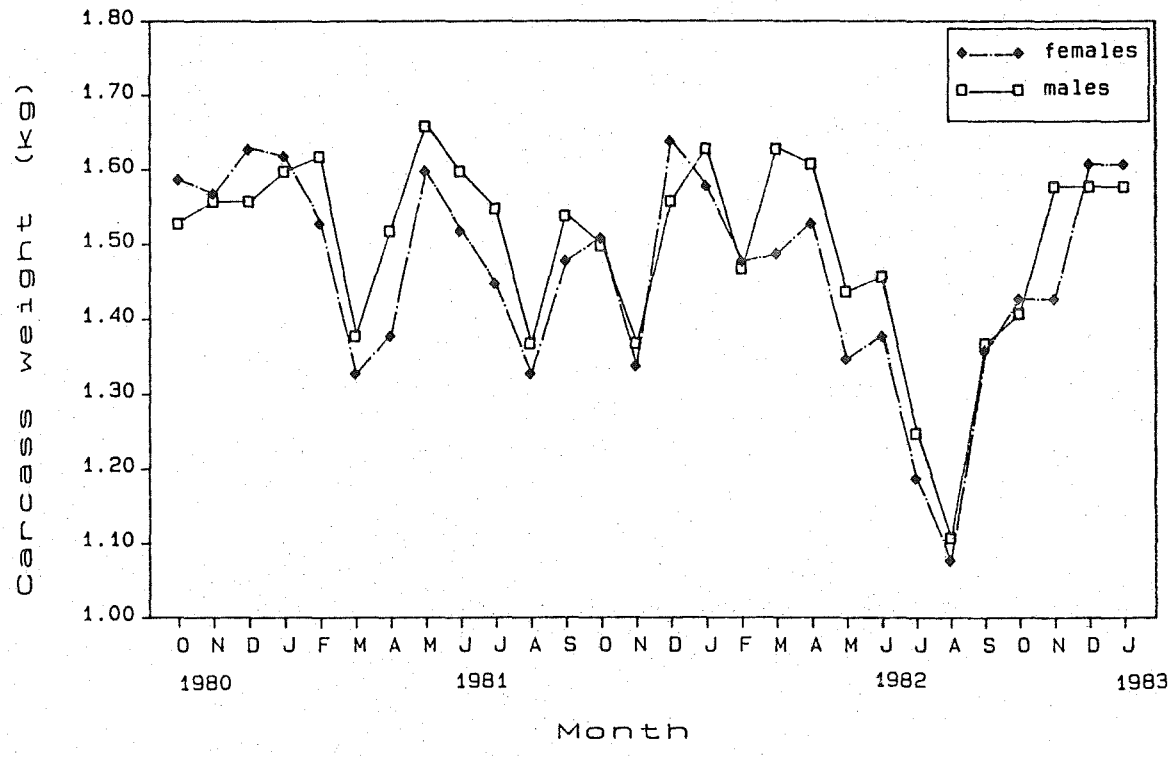

Figure 16.4 Mean carcass weight for adult male and female rabbits.

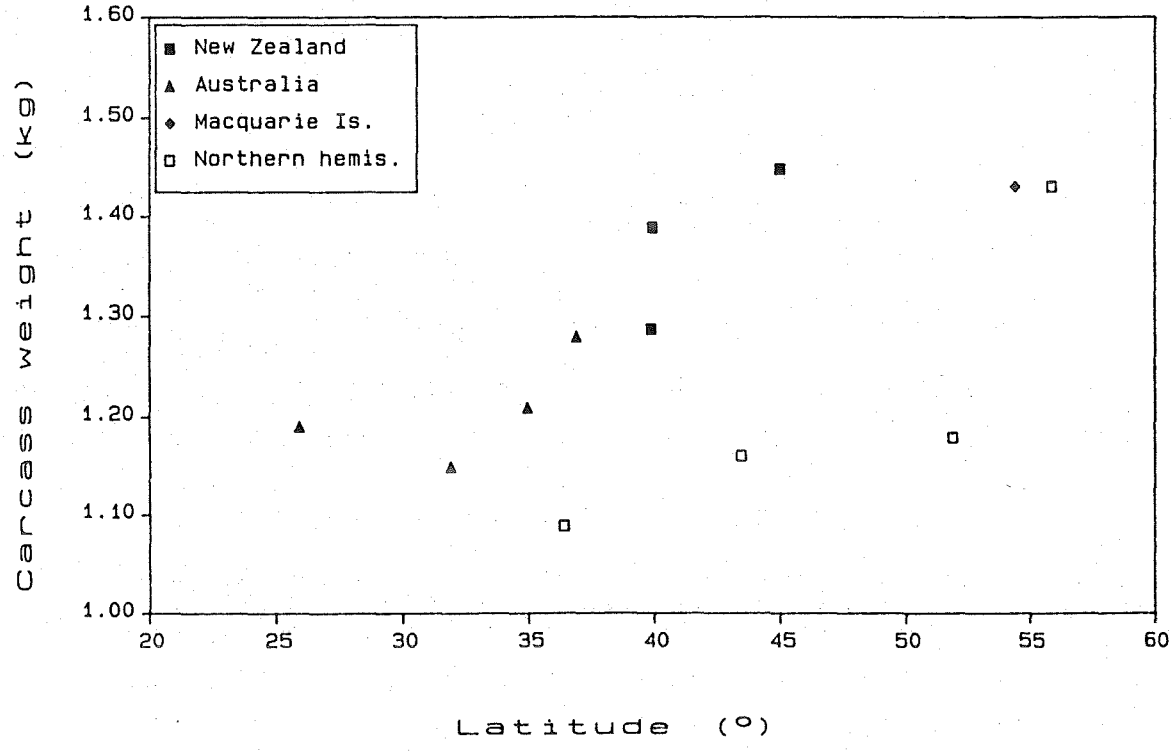

Figure 16.5 Variation in adult carcass weight between rabbit populations at different latitudes.

when data from each hemisphere are considered separately. Rogers (1979) suggested that the greater size attained by rabbits in Australia compared with southern France may be due to the inclusion of domestic stock in the initial introductions. However, the present wild population in Australia is considered to have originated solely from wild stock (Rolls 1969, Myers 1971). A more plausible explanation for the variation between northern and southern hemisphere populations is that genetically larger rabbits were chosen for the original liberations, thereby resulting in the present pattern.

16.2.2 Fat-related condition

Two methods were employed to quantify fat-related condition, the KFI and Riney's visual index of abdominal fat. Whereas KFI estimates require careful autopsy and subsequent measurement of material, Riney's visual index is easily performed in the field by inspection only. However, the visual method is subjective and may not be as reliable as the KFI.

The main disadvantage associated with the use of the KFI is the seasonal variation in kidney weight, the bench-mark by which fat levels are corrected for body weight differences. Seasonal fluctuations in kidney weight are substantial in cervids and distort the apparent seasonal trends in condition indicated by the KFI (Batcheler and Clarke 1970, Dauphine 1975). In addition, Van Vuren and Coblentz (1985) revealed that kidney weight was not consistently proportional to body weight for feral sheep. This suggests that age (and therefore size) differences between populations may cause variation in KFI estimates. Therefore, these aspects were examined before the data could be analysed for trends between sex and age classes, and seasons.

Linear regression was used to evaluate the relationship between kidney weight and carcass weight (Figure 16.6). Data from only one period (February-April 1982) were used in order to eliminate the possibility of seasonal variation influencing the result. This period was chosen because of sample size (n=266) and the inclusion of rabbits from all age classes.

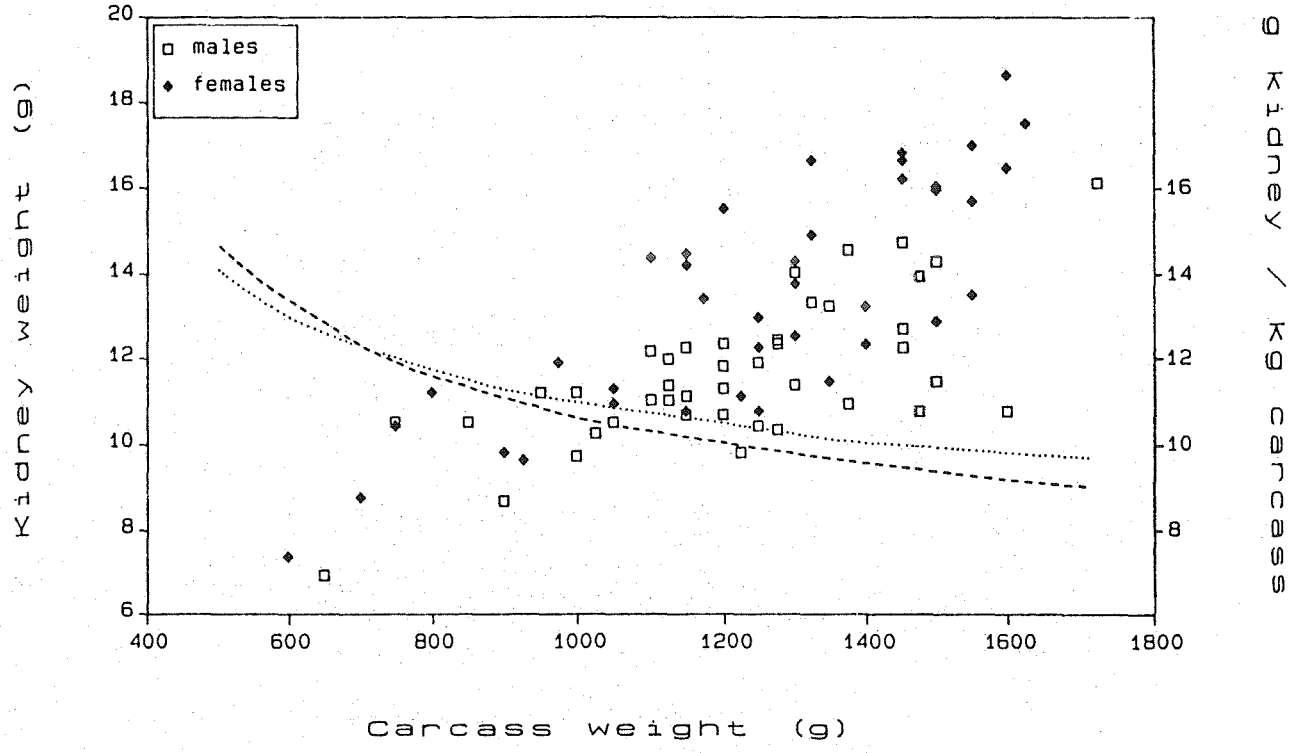

Figure 16.6 Relationship between kidney weight and carcass weight for male (dashed line) and female (dotted line) rabbits collected between February and April 1982; individual data points for February are also shown.

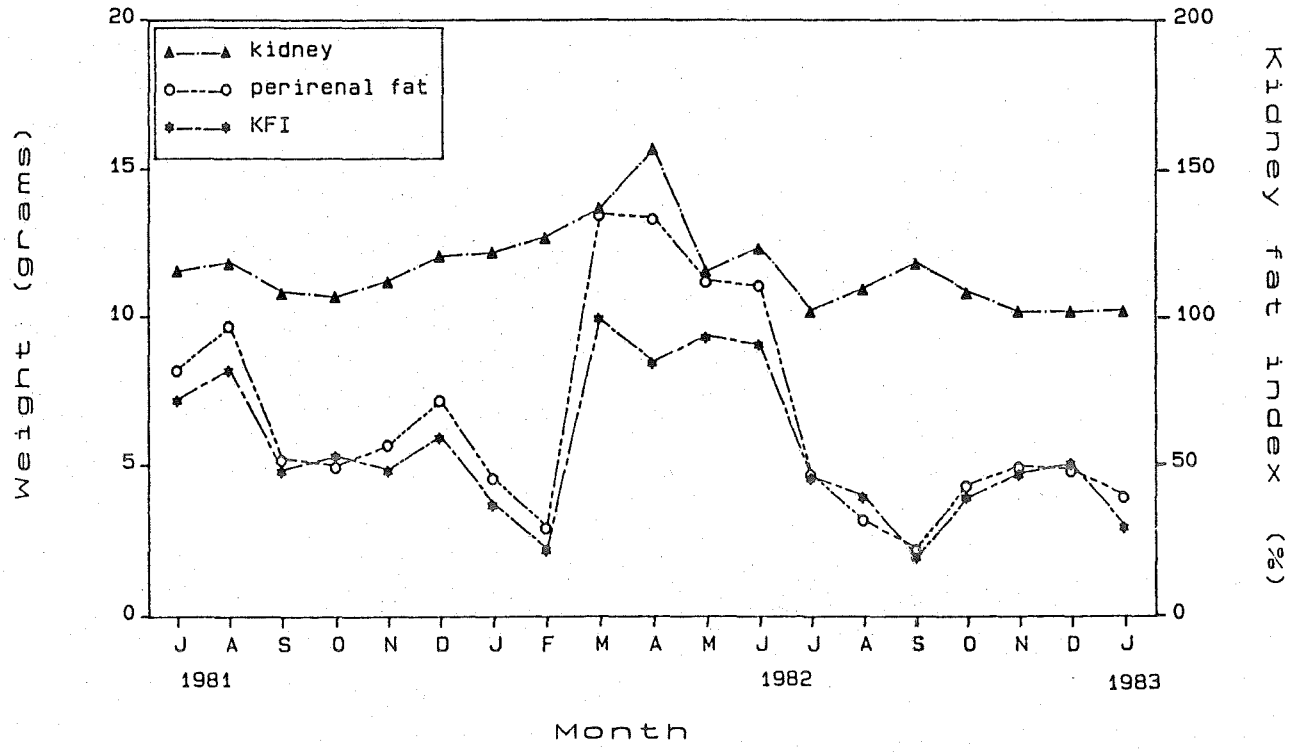

Figure 16.7 Monthly fluctuations in kidney weight, perirenal fat weight, and the kidney fat index (KFI) for adult male rabbits.

Regressions for male and female rabbits were significantly different (ANCOVA, $F=11.03, p<.001$) so the sexes were treated separately. The relationships between paired kidney weight (y) and carcass weight (x) for males and females respectively were:

$$y = 3.99 + 0.00673\ x \qquad (n=135, r=0.75)$$

$$y = 3.16 + 0.00782\ x \qquad (n=131, r=0.76)$$

The non-zero y-intercepts for the regression equations confirm that kidney weight is not directly proportional to carcass weight. Comparison of monthly means revealed that kidney weight varied from 0.7-1.1% of carcass weight for male rabbits and 0.7-1.3% for females between the various samples. The true relationship between kidney weight and carcass weight is indicated by the dashed lines calculated from the regression equations (see Figure 16.6); constant proportionality would be indicated by a horizontal line. Instead, the dashed lines curve upwards at lower weights, indicating that smaller rabbits have proportionately larger kidneys. Cabon-Raczynska (1964) observed that the weight of the kidneys varied from 0.37-0.85% of body weight and that the pattern of weight increase for the kidneys was negatively allometric. The separate regressions for males and females reveal similar kidney weights for rabbits less than 1000 g but at greater weights females have proportionately larger kidneys than males. In addition to Van Vuren and Coblentz's (1985) evidence for feral sheep, Johns et al. (1980) reported a similar linear regression between kidney weight and body weight for white-tailed deer **Odocoileus virginianus.** Analysis of all adult rabbits shows that the sexual dimorphism in kidney weight is highly significant ($t=9.96, p<.001$) despite the fact that females have lighter carcass weights ($t=3.68, p<.001$).

Considerable seasonal fluctuations occurred for kidney weight (ANOVA, $F=8.57, p<.001$) (Table 16.2). Although no sex differences in kidney weights existed during autumn and winter, females had significantly heavier kidneys ($p<.01$) during spring and summer months. Surprisingly, the fluctuations in kidney weight had little adverse effect on the KFI as the data for adult male

rabbits indicates (Figure 16.7); the changes in mean KFI's between consecutive months closely track the pattern for perirenal fat weight. The pattern for adult females is similar although they exhibit slightly greater variability in kidney weight (CV=19.5%) than male rabbits (CV=16.5%). Seasonal variation in kidney weight for rabbits and hares (Flux 1971) is substantially less than for cervids (Batcheler and Clarke 1970, Dauphine 1975) and this may account for the less significant effect on KFI values.

Table 16.2 Seasonal variation in mean paired kidney weight for adult male and female rabbits.

Season	Males n	Males Kidney wt. (g)	Females n	Females Kidney wt. (g)
Summer	139	11.21 (±0.29)	97	13.93 (±0.58)
Autumn	56	13.03 (±0.70)	47	13.18 (±0.77)
Winter	206	11.79 (±0.28)	163	12.07 (±0.33)
Spring	190	11.24 (±0.20)	193	13.17 (±0.34)

n = sample size, 95% confidence limits in brackets

A number of reasons have been proposed for seasonal fluctuations in kidney weight including inanition and reduced forage intake (Batcheler and Clarke 1970), metabolic activity (Flux 1971), and body water kinetics or heat stress (Dauphine 1975). As the lowest mean kidney weights for rabbits did not coincide with the lowest condition indices recorded, inanition is probably not an important influence of kidney weight in rabbits. Kidney weight appears to be closely related to the physiological requirements and metabolic activity of the rabbit; it is greatest during the breeding season and immediately afterwards when a marked increase in fat reserves occurs. This pattern is more exaggerated among females, reflecting the additional physiological stress of reproduction.

In order to correct for seasonal and size-related fluctuations in kidney weight, the data were pooled and the mean paired kidney weight for all adult rabbits was calculated (12.23 g). A series of correction factors based on the monthly means were calculated in relation to the overall mean weight. These correction factors were then applied to each month's data to standardise kidney weights between the samples. KFI values calculated from the original data together with adjusted KFI estimates from the standardised data exhibit similar trends (Figure 16.8). The use of a single correction factor for both sexes tends to reduce the variation accounted for by sex (F=0.06 for adjusted KFI's, cf. F=0.92 for the uncorrected data).

Variation in condition indicated by the adjusted KFI values was produced by a number of factors (Table 16.3). Season and age accounted for much of the variation while the effect of sex was not significant. However, two-way interactions between sex and both season and age class produced significant effects.

Table 16.3 Analysis of variance for heterogeneity in adjusted KFI's with respect to sex, age class and season.

Source of variation	Sum of squares	df	Mean square	F	Sign.
Sex	190.6	1	190.6	0.16	NS
Age class	136104.6	4	34026.2	28.57	p<.001
Season	365604.8	3	121868.3	102.32	p<.001
Sex x age class	14310.6	4	3577.4	3.00	p<.001
Sex x season	43485.3	3	14495.1	12.17	p<.001
Age class x season	62339.8	12	5195.0	4.36	p<.001
Residual	2158532.4	1813	1190.6		
Total	2793795.5	1840	1518.4		

The seasonal trend in perirenal fat levels is similar to that reported by Martin (1977) for abdominal fat reserves of rabbits in a semi-arid environment

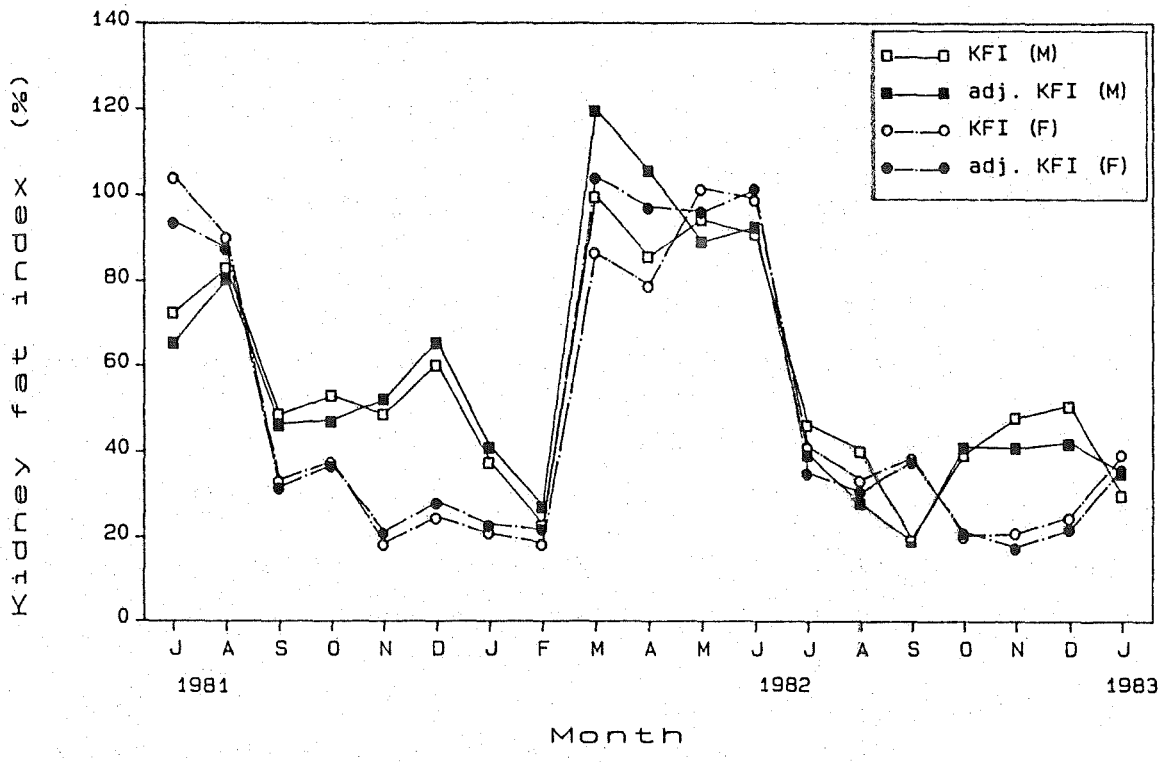

Figure 16.8 KFI and adjusted KFI (corrected for seasonal and size-related variation in kidney weight) values for adult male (M) and female (F) rabbits.

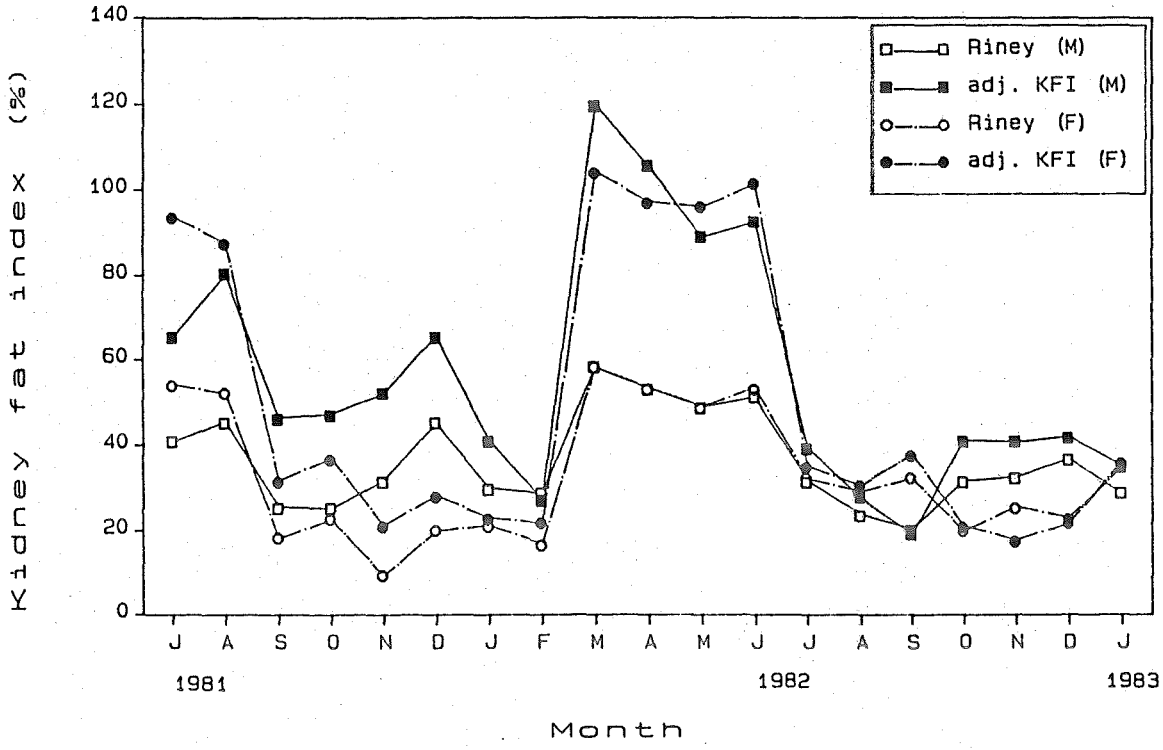

Figure 16.9 Comparison of adjusted KFI values and Riney's visual index of condition for adult male (M) and female (F) rabbits.

in western New South Wales. Fat levels are greatest during autumn and winter months followed by a rapid decline to low levels during spring and summer. Fat indices for females fall to lower levels than those for males during this period, probably due to the greater metabolic demands on females during the breeding season. Towards the end of summer, coinciding with the cessation of breeding, fat levels begin to increase for both males and females. This pattern confirms Flux's (1971) suggestion that fat levels are not related to the availability of food but rather trace the metabolic requirements of the animal. Bamford (1970) found a similar seasonal trend for possums although the pattern of variation between males and females differs from that for rabbits, probably due to the markedly different reproductive characteristics of possums.

Perirenal fat reserves were highest during that part of the year when the available vegetation was extremely limited and environmental conditions were often severe. During this period stored energy in the form of fat is required to allow rabbits to cope with the increased metabolic demands of extremely cold weather or the onset of the breeding season. Conversely, fat reserves were lowest when the environment was most favourable and the food supply plentiful. Therefore, it appears that fat levels in rabbits may reflect metabolic requirements and physiological adaptation to the environment rather than the availability of resources to produce fat reserves. For this reason, fat-related condition is probably of little use as a predictive indicator of control operation success (see also section 12.3).

Flux (1971) reasons that wild animals subject to predation minimise the time they spend feeding and therefore are unlikely to carry unnecessary fat; alternatively, fat reserves have a specific function and do not simply accumulate because food is abundant. However, this view must be tempered with Martin's (1977) observation that variations in fat reserves can provide a measure of relative environmental favourability. Together with evidence for a relationship between fat reserves and the rate of increase of a population

(Caughley 1967, Bamford 1970, Martin 1977) it could be concluded that seasonal patterns indicate physiological adjustment and metabolic needs whereas instantaneous differences between populations reflect environmental favourability. Fluctuations in condition are therefore influenced by hormonal factors and to a lesser extent by direct environmental control.

Mean monthly values of Riney's visual index of condition were plotted together with adjusted KFI means for adult males and females (Figure 16.9). The correlation coefficients between these condition indices were highly significant for both sexes ($p<.001$). As a further check Spearman's rank correlation coefficients were calculated and these confirmed that the two methods of assessing condition produce similar results for male ($r_s=0.83$, $p<.001$) and female rabbits ($r_s=0.85, p<.001$). Therefore, provided the standard procedures adopted during this study are followed, a visual estimate of fat-related condition can provide equally useful results as more laborious techniques requiring careful autopsy and measurement of material. Care is needed to ensure that judgement of fat levels does not vary between different observers or the same observer at different times.

If the KFI is used, size-related variation in results may be avoided by examining the data according to age class. Seasonal fluctuations do not produce the substantial distortions on the KFI observed for cervids (Batcheler and Clarke 1970, Dauphine 1975) and feral sheep (Van Vuren and Coblentz 1985). In addition, abdominal fat reserves in rabbits rarely fall below the level where the KFI is less reliable than other indicators of condition such as marrow fat (Martin 1977, Warren and Kirkpatrick 1978). Therefore, the KFI is a reliable indicator of fat-related condition for rabbits and probably other lagomorphs (Flux 1971).

16.2.3 Weight-length relationships

Total weight and total length data were log transformed and regressed to obtain the mean relationship between weight and length. Because of the sexual

dimorphism in body dimensions (see section 16.2.1), males and females were treated separately. The resulting standard weight equations are similar to those obtained by Bamford (1970) and Fraser (1979) for possums. The equations for male and female rabbits respectively are:

$$w = 0.00149\ L^{2.62542}$$

$$w = 0.00094\ L^{2.70033}$$

where w = total weight in grams, and

L = total length in cm.

An attempt was made to correct for the inclusion of the tail in the total length measurement; a constant, equivalent to the estimated average tail length (4.5 cm), was subtracted from all total lengths. However, the regression exponents obtained were less compatible with the general cubic relationship between body weight and length than the uncorrected data. Consequently, the regressions using total length were retained as the most reliable assessment of standard weight.

Standard weights for each rabbit were obtained by applying the observed total length data to the male or female regression equations. The ratio of the actual total weight to the estimated standard weight was then expressed as a percentage. This weight-related condition value indicates the relationship between a rabbit's actual weight and its theoretical expected weight based on total length. A value less than 100% indicates that the rabbit is lighter than expected for its length whereas a value greater than 100% suggests that the rabbit is in better than average condition.

A strong relationship between weight-related condition and age was evident (Figure 16.10). Rabbits in the 0-6 month age class were still growing and because linear dimensions increase quicker than weight (see section 16.2.1) young rabbits appear to be in poor condition. The higher values exhibited by females in the >12 month age classes are due to higher total weights associated with pregnancy. In view of their greater carcass weights and lower mean length, males would be expected to exhibit higher

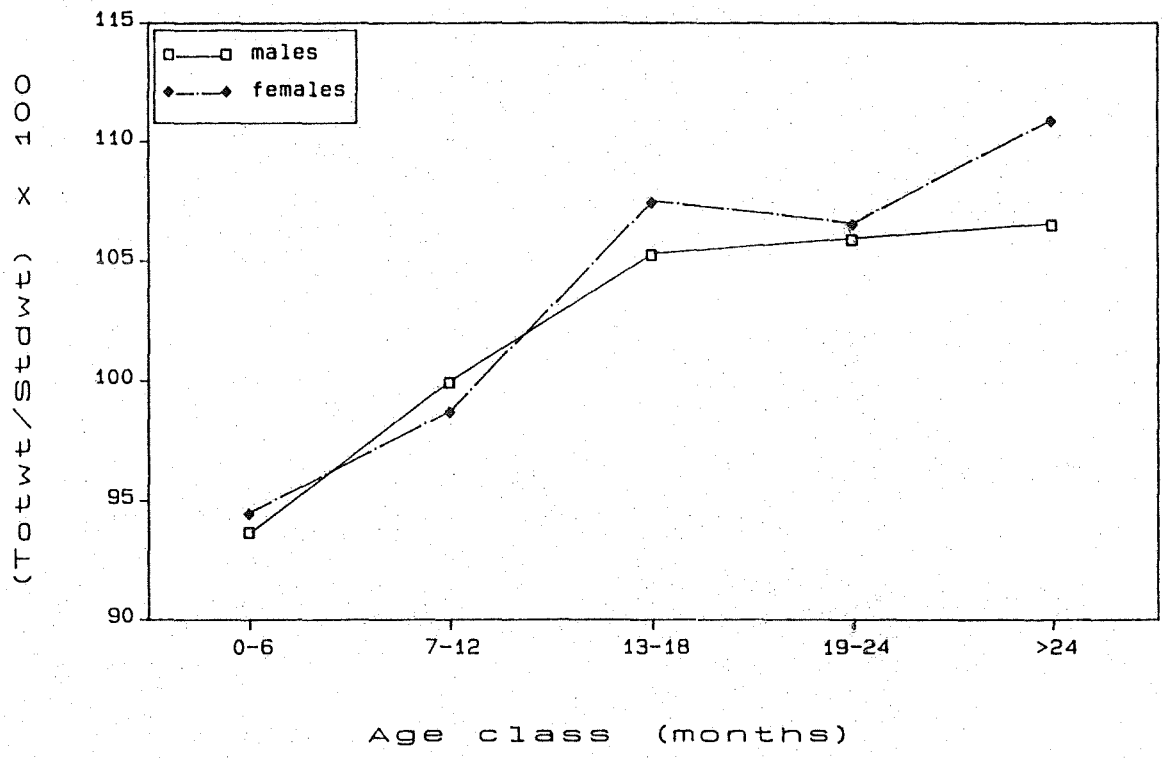

Figure 16.10 Relationship between weight-related condition and age for male and female rabbits according to the formula (total weight/standard weight) x 100.

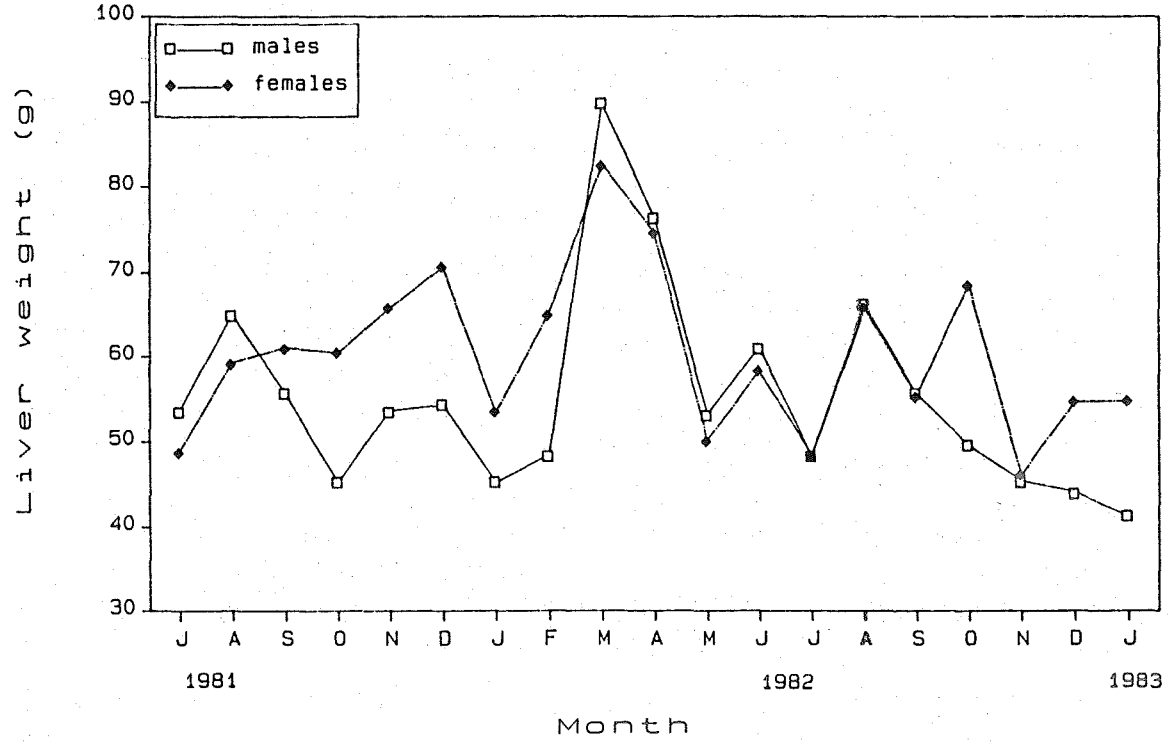

Figure 16.11 Seasonal fluctuations and sexual dimorphism in liver weight for adult male and female rabbits.

weight-related condition values if the data for pregnant females were removed.

The weight-related condition estimates were regressed against KFI's for adult males and females separately. Whereas the relationship for males is linear and highly significant ($r=0.49, p<.001$), females do not exhibit any clear pattern ($r=0.04$, NS). This confirms the suggestion that the weight-length relationship for female rabbits is obscured by the inclusion of pregnant females in the calculations. When the data were graphed by month the pattern for adult female rabbits was somewhat erratic in comparison to that for males. Weight-length relationships are of limited value as condition indices for rabbits, especially if young rabbits are not excluded from the analyses.

16.2.4 Liver weight

Substantial sexual dimorphism existed among adult rabbits for liver weight (Figure 16.11). While there was little variation in liver weight between males and females during autumn and winter months (ANOVA, $F=1.11$, NS), female rabbits had significantly heavier livers during spring and summer (ANOVA, $F=140.65, p<.001$).

The relative weight of the liver changed with the age of the rabbit (Table 16.4). The pattern exhibited, where older rabbits generally have proportionately smaller livers, was similar to that for kidney weight (see section 16.2.2). Relative differences between males and females for liver weight were also similar to kidney weight trends. The kidneys and liver are closely associated with and integrate many metabolic processes (Marshall and Hughes 1980), and therefore the patterns of weight change reflect the variation in metabolic requirements between young and adult rabbits as well as between males and females.

Table 16.4 Relative weight of the liver with respect to carcass weight according to sex and age class.

Age class (months)	Relative weight (%) Males	Females
0–6	4.07 (194)	4.33 (180)
7–12	4.44 (397)	4.57 (360)
13–18	3.66 (228)	4.22 (190)
19–24	3.68 (75)	4.12 (84)
>24	3.88 (76)	4.39 (36)

sample size in brackets

17 REPRODUCTION

17.1 Introduction

Several reproductive characteristics of lagomorphs differ markedly from basic mammalian life history tactics (Millar 1977, 1981). Relative to other eutherian mammals, lagomorphs exhibit extremely rapid foetal and neonatal growth rates, short gestation periods, and low maternal investment in generally large litters (Swihart 1984). The nearly cosmopolitan distribution of lagomorphs (Walker 1964) confirms the success of their high fecundity life history strategy. Despite the similar overall pattern of reproduction among lagomorphs, considerable variation of several reproductive parameters exists within the order (see Myers 1971, Flux 1981, Swihart 1984). Whereas body size and phylogeny account for some of this variation, environmental severity and seasonality are also important forces influencing reproductive characteristics in lagomorphs (Swihart 1984). For instance, nutritional factors contribute to the relatively high foetal growth rates in lagomorphs through their influence on basal metabolic rates (McNab 1980).

While the rabbit's basic reproductive strategy evolved to maximise productivity in its original western Mediterranean environment, it is an opportunist breeder (Poole 1960, Myers and Poole 1962, Wood 1980) and variations on the ancestral reproductive theme occur within the numerous environmental types it now inhabits. The rabbit's adaptation to and remarkable productivity in many new environments partly accounts for its pest status in some of these areas. In its original range and other environments with characteristically distinct seasons, often with low or restricted rainfall regimes, the rabbit is usually a seasonal breeder (e.g. Myers 1971, Andersson, Dahlback and Meurling 1979, Rogers 1979, King et al. 1983). In climatically more stable environments the rabbit can breed all year round (e.g. Bell 1977, Williams and Robson 1985, Gibb et al. in press). There are many exceptions to these patterns, however, as complex relationships between latitude and

numerous environmental factors influence the rabbit's reproductive strategy (see Sadleir 1969 for a review).

While the ultimate determinant of rabbit population density is the mortality rate (Tyndale-Biscoe and Williams 1955, Myers 1971, Gibb et al. 1978) considerable short-term fluctuations in density may occur because of the rabbit's opportunistic breeding strategy, allowing it to take advantage of favourable environmental conditions to reproduce (Wood 1980). Previous studies on the rabbit reveal a wide range of values for various reproductive parameters including length of the breeding season, age at sexual maturity, litter size, and annual productivity (e.g. Brambell 1944, Watson 1957, McIlwaine 1962, Lloyd 1963, Myers 1971, Andersson, Dahlback and Meurling 1979).

The breeding pattern exhibited by rabbit populations in Central Otago has not been documented previously. In view of environmental similarities with the rabbit's original homeland and many parts of inland Australia, examination of the reproductive biology of the rabbit in this region was of considerable comparative value.

17.2 Results

Several reproductive parameters are examined in detail in this section and although they are all intrinsically linked, it is easier to treat them separately. The overall reproductive pattern that emerges for Central Otago, and its adaptive significance, is discussed in the final section of this chapter and compared with previous studies.

17.2.1 Breeding season

The onset and duration of the breeding season were indicated by the proportion of females visibly pregnant or lactating each month (Figure 17.1). All females at least 16 weeks old were included in this analysis. This was the youngest age at which females became pregnant, although some females older

than 16 weeks may not have been sexually mature.

The pattern of pregnancies in Central Otago is highly seasonal with almost all breeding occurring between September and February although there is some variation between years. Part of the variation between consecutive months during the breeding season is probably due to the wide variety of areas from which autopsy samples were collected. Differences in altitude, population density, and habitat quality are known to produce variation in the reproductive potential of rabbit populations through their effects on the duration of the breeding season (e.g. Watson 1957, Poole 1960, Wodzicki and Darwin 1962, Myers 1971). The 1980/81 breeding season almost certainly began before the first autopsy sample was collected in October 1980. This is confirmed by the high lactation rate in October 1980. Rabbits pregnant for the first time do not begin to lactate until a few days prior to parturition (Brambell 1942).

A noticeable feature of rabbit reproduction in Central Otago is the abrupt start to the breeding season; the proportion of females pregnant and lactating increases sharply over a short period (see Figure 17.1). Generally, the end of the breeding season is not as abrupt, with the proportion of females pregnant and lactating declining during summer before breeding ceases completely around March. The two isolated autopsy samples collected in 1983 suggest that the 1982/83 breeding season lasted longer than in previous years and the 1983/84 breeding season commenced earlier than usual. Rainfall during the 1982/83 summer was approximately double that of the previous two summers and this may have extended the growing season for vegetation. Rainfall totals and mean temperatures in the months prior to July 1983 were not appreciably different from the previous two years so the cause of the early start to breeding in 1983 is unclear.

The values in Figure 17.1 underestimate the actual pregnancy rate because pregnancy is not detectable during approximately the first five days of gestation (Brambell 1942, Adams 1960). By about the fifth day of gestation the

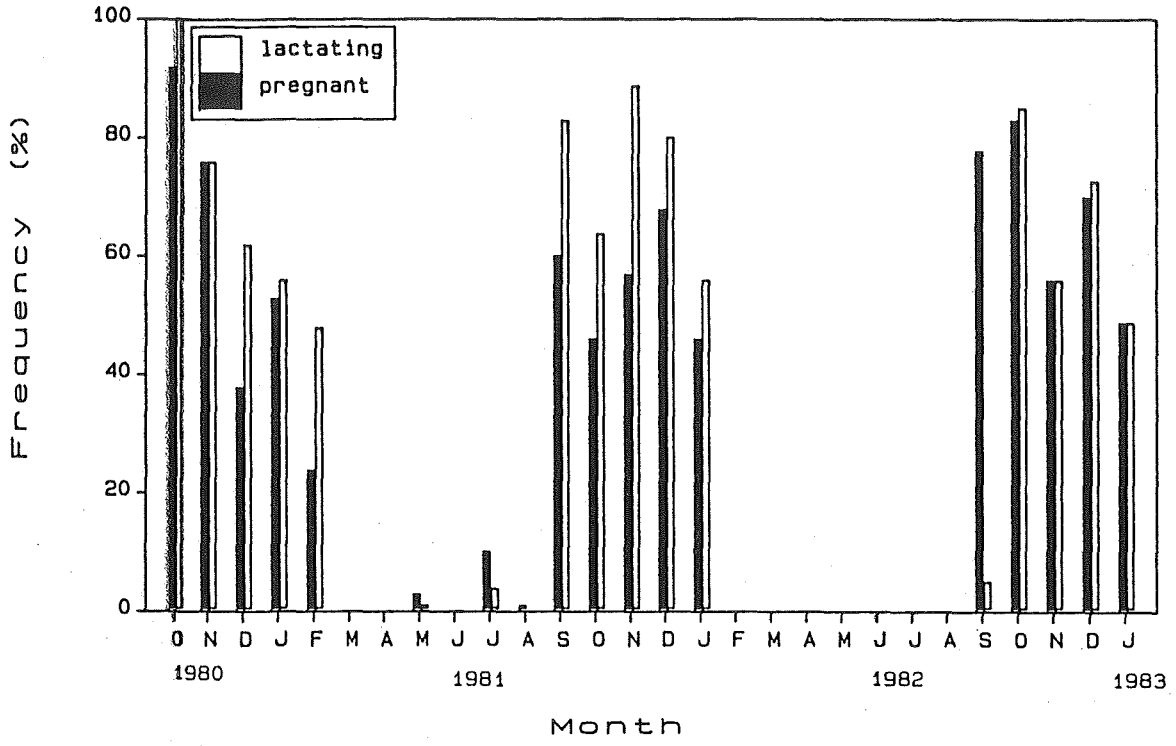

Figure 17.1 Proportion of female rabbits (≥16 weeks old) visibly pregnant or lactating, by month.

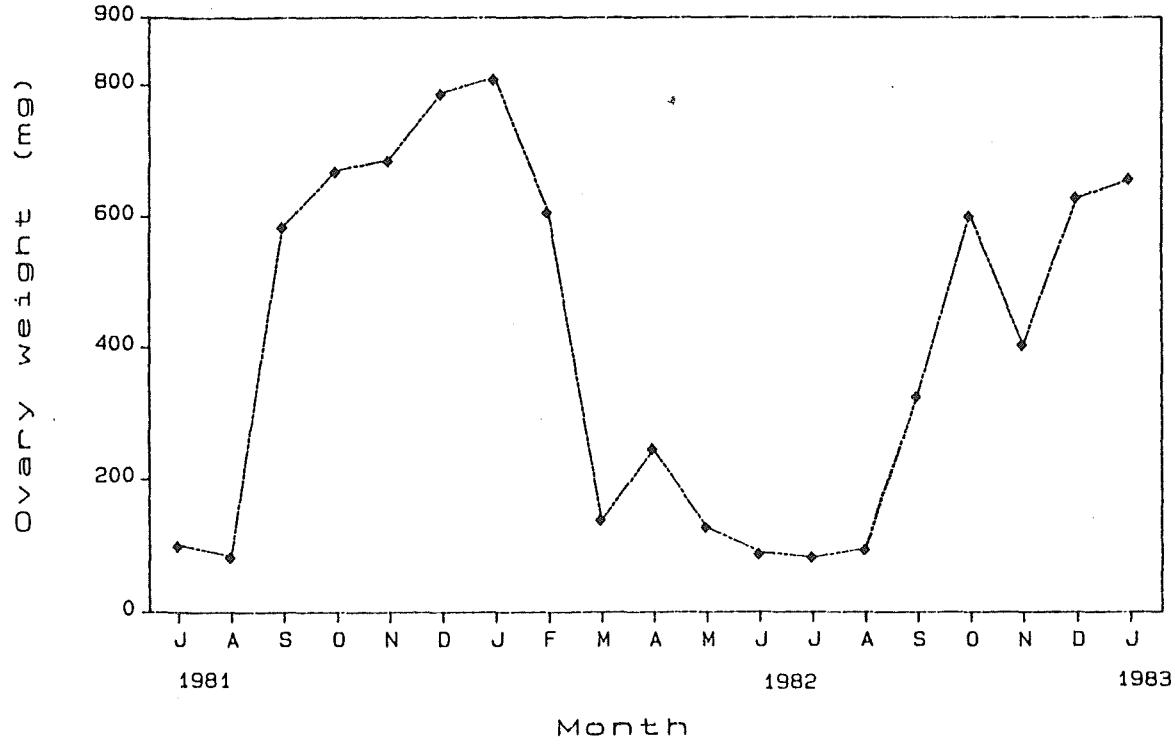

Figure 17.2 Seasonal variation in mean paired ovary weight of adult female rabbits.

blastocysts become attached and form macroscopically visible swellings on the uterus. Therefore, based on an average gestation period of 30 days (Ward 1971), the actual pregnancy rate can be obtained if the observed rate is multiplied by 1.2 (30/25). Using this factor to correct the observed pregnancy rates, it appears that the maximum number of females were pregnant on only one occasion (October 1980). However, the possible inclusion in some samples of females who had not reached sexual maturity may have depressed the actual pregnancy rate.

From a total of 1491 female rabbits at least 16 weeks old, 27% were visibly pregnant and 26% were lactating. Between September and February 60% of females were visibly pregnant. Correcting for the initial stages of gestation when pregnancy is not detectable, this converts to an actual pregnancy rate of 72% during the breeding season. The annual pregnancy rate for the year June 1981 to May 1982 was 28%.

The seasonal reproductive pattern and the inherent variation between the samples are also reflected in the cycle of ovary weight observed for adult female rabbits (Figure 17.2). Ovary weight increases rapidly at the beginning of the breeding season and remains at a fairly constant level (paired ovary weight of 600-800 mg) throughout the breeding season, before a marked regression in weight occurs through autumn to the low levels observed during the winter months (paired ovary weight of about 100 mg). The seasonal variation was highly significant (ANOVA, $F=145.24$, $p<.001$).

17.2.2 Male fertility

Previous workers have used several indices of fertility in male rabbits including testis position, testis weight, and the presence of sperm (Brambell 1944, Watson 1957, Poole 1960, Myers and Poole 1962, Shipp et al. 1963, Cooke 1974, Bell 1977, Andersson, Dahlback and Meurling 1979, Rogers 1979, J T Martin unpub.). Rogers (1979) used all three methods and demonstrated a high degree of consistency in the results provided by each of these indices.

Data collected during this study allowed examination of male fertility according to testis position and testis weight. In the rabbit the testes may be found in the abdomen or the scrotum. Testes found intra-abdominally may produce sperm and testosterone but the sperm will not be viable (Marshall and Hughes 1980). For most eutherian mammals the conditions necessary for sperm to be viable only occur when the testes are scrotal (Hildebrand 1974).

The youngest age at which male rabbits were found with scrotal testes was 16 weeks but this was uncommon. Most males with scrotal testes were at least 26 weeks old. The highest proportion of males with scrotal testes was found in the 13-18 month age class, although males in the 19-24 month age class exhibited the greatest testis weight (Table 17.1). Fertility appeared to decrease slightly for male rabbits older than 24 months. The highest proportions of males with scrotal testes coincided with the peaks of pregnancy although a considerable proportion of males had scrotal testes outside the breeding season (Figure 17.3a). Some males with scrotal testes were found in all months, the lowest level being 3% in March 1982.

Table 17.1. Variation in testis position and testis weight with respect to age.

Age class (months)	n	Number with scrotal testes	%	Mean paired testis wt. (g)
0-6	194	38	19.6	1.55
7-12	409	158	38.6	3.86
13-18	232	124	53.4	4.47
19-24	79	33	41.8	4.62
>24	73	31	42.5	4.21

n = sample size

Testis weights of adult male rabbits were high in winter and spring 1981 but declined through summer and autumn to very low levels in late winter 1982 (Figure 17.3b). The low paired testis weight in March 1982 coincides with the

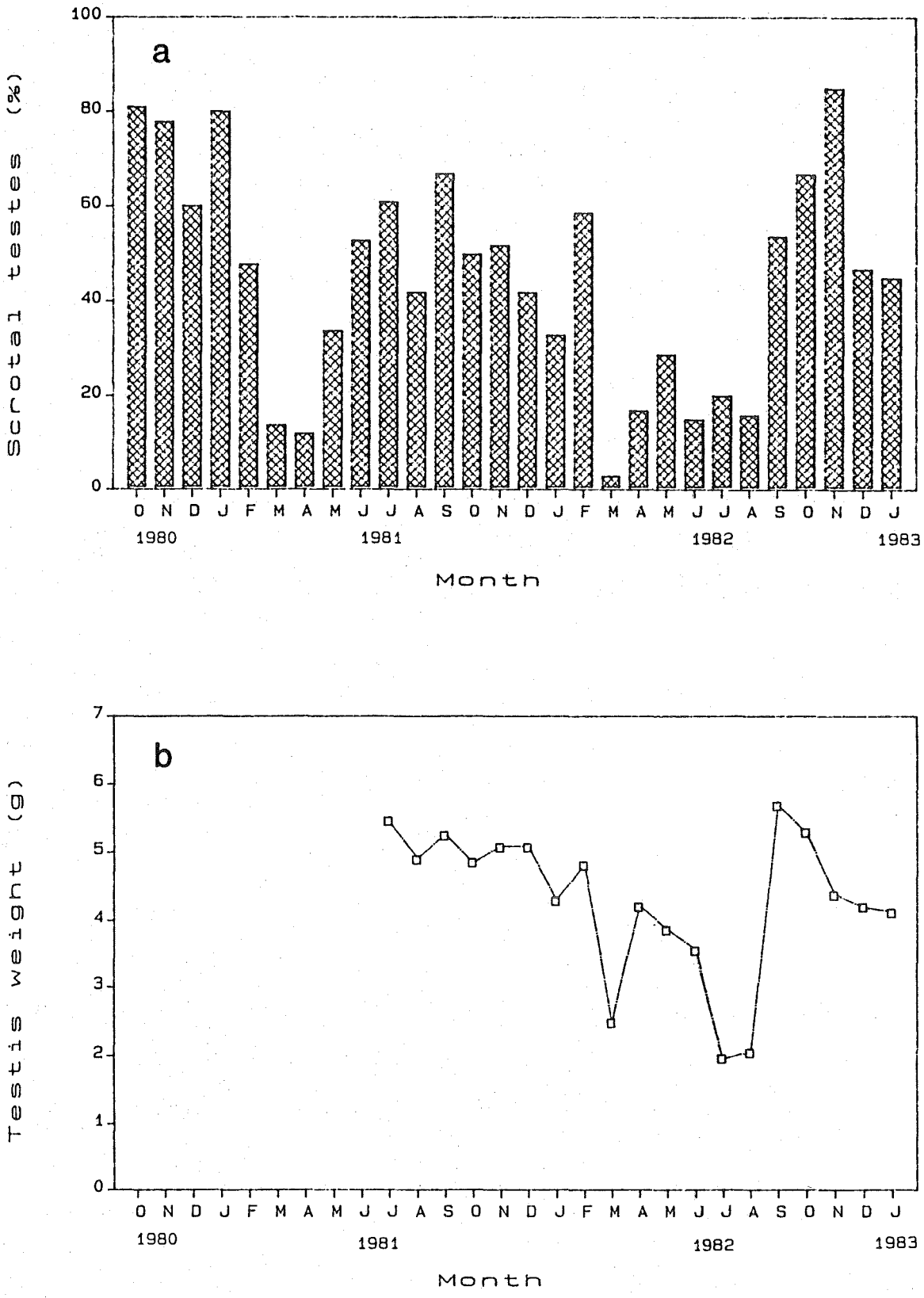

Figure 17.3 (a) Proportion of male rabbits (≥16 weeks old) with scrotal testes and (b) mean paired testis weights for adult male rabbits.

lowest proportion of males with scrotal testes. Significantly, no pregnant females were found in March 1982, compared with 46% for the previous month. A marked increase in testis weight occurred between August and September 1982 but thereafter a gradual decline occurred. The seasonal variation in testis weight was highly significant (ANOVA, $F=18.22, p<.001$). Heavy testes were usually scrotal, firm in texture, and light-coloured. Regressing testes were more commonly abdominal, considerably lighter, flaccid, and reddish-brown in appearance. Variation between consecutive monthly samples in testis weight and the proportion of males with scrotal testes followed a similar pattern to that for pregnancy and ovary weight, confirming the variability between rabbit populations from different areas within the Alexandra Pest Destruction Board district.

The difference in male fertility between the 1981/82 and the 1982/83 breeding seasons is reflected in both the testis position and testis weight data. Fertile males were present for a considerable period prior to the breeding season in 1981. In contrast, the increase in male fertility in 1982 coincided with the onset of breeding.

17.2.3 Female fertility

The number of ova ovulated at each oestrus represents the potential litter size. Development of ruptured follicles into corpora lutea provides a useful indicator of female fertility. In the rabbit corpora lutea persist through pregnancy but regress rapidly after parturition (Brambell 1944, Watson 1957) and are easily counted macroscopically.

Ovaries of 404 sexually mature females were examined. The number of corpora lutea ranged from one to eleven, with six being the most frequent number found. The mean number of corpora lutea was 6.29 over the entire study but this varied considerably according to season as well as the age and carcass weight of the female.

As there is an unequal representation of months, data from the July 1983 sample are excluded from most analyses. Female fertility was significantly greater during the 1981/82 breeding season (6.84 corpora lutea per female) compared with the 1982/83 breeding season (6.19 corpora lutea) ($t=3.38$, $p<.001$). The frequency distribution of corpora lutea counts was also markedly different (Figure 17.4). More than 62% of females had seven or more corpora lutea during the 1981/82 season compared with only 38% for the 1982/83 season.

Female fertility exhibited an increase following the onset of breeding to a peak around the middle of the breeding season (Table 17.2). The decline in fertility towards the end of the breeding season was partly due to young females breeding for the first time. However, even experienced females exhibited some decline in fertility during the final months of each breeding season. The lowest number of corpora lutea per female (4.93) was observed for the July 1983 sample which included a large proportion (75%) of females breeding for the first time.

Table 17.2 Corpora lutea counts for all sexually mature females.

Month	No. of females examined	Mean no. of corpora lutea
September 1981	42	6.88
October	14	7.29
November	43	7.07
December	33	7.27
January 1982	14	6.86
February	24	5.67
September 1982	50	5.18
October	40	6.83
November	8	6.38
December	32	7.12
January 1983	30	6.60
March	19	5.79
July 1983	55	4.93

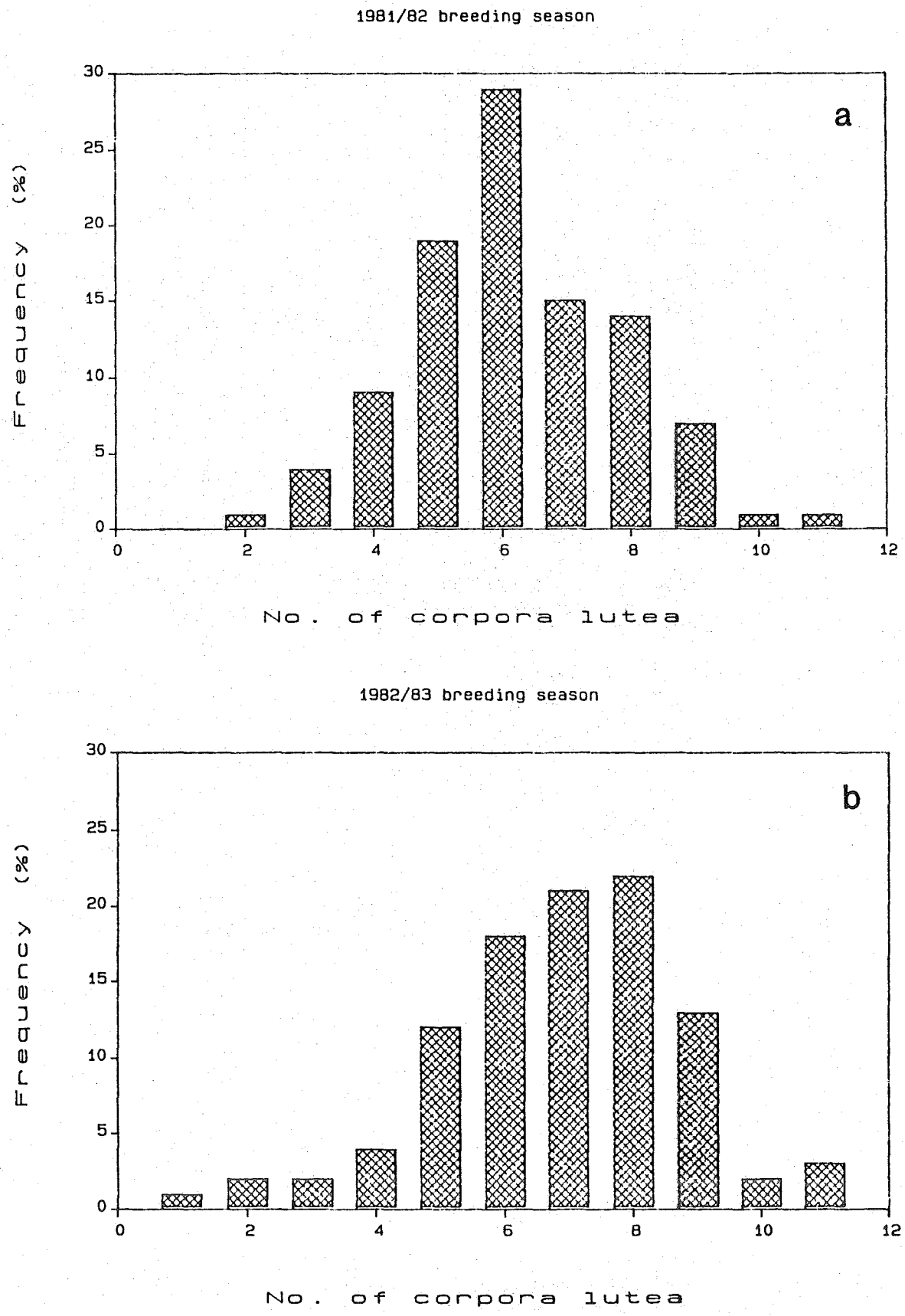

Figure 17.4 Frequency distribution of the number of corpora lutea for (a) the 1981/82 breeding season and (b) the 1982/83 breeding season.

Although fertility levels may vary between years, the seasonal trends are remarkably similar as results for the mean number of embryos per female show (Figure 17.5). The highest female fertility occurs during October-December. Extensions of the breeding season into early autumn are usually accompanied by a small rise in female fertility. The lowest levels of fertility occur among females during winter months, immediately prior to the main onset of breeding. This basic seasonal pattern is also reflected in data from other studies, both in Central Otago (J Bell unpub.) and elsewhere (e.g. Watson 1957, Andersson, Dahlback and Meurling 1979) (see Figure 17.5).

The age of the female was an important determinant of fertility (ANOVA, $F=4.93, p<.001$) (Table 17.3). Rabbits up to 12 months old were usually in their first breeding season and exhibited significantly lower fertility than rabbits greater than 12 months old. Corpora lutea counts and embryo counts exhibited similar trends with respect to female age (Figure 17.6). Female fertility appears to decline slightly in older rabbits, as observed for male fertility.

Table 17.3 Variation in the number of corpora lutea with respect to age.

Age class (months)	n	Mean no. of corpora lutea	Standard error
0-6	26	5.88	0.19
7-12	104	6.29	0.18
13-18	95	7.14	0.16
19-24	42	6.86	0.25
>24	21	6.81	0.36

n = sample size

The number of ova ovulated was strongly correlated with the carcass weight of the female ($r=0.48, p<.001$), a relationship obviously influenced by age. However, even among adult females weight was still an important factor ($r=0.39, p<.001$). Heavier adult females had significantly higher fertility

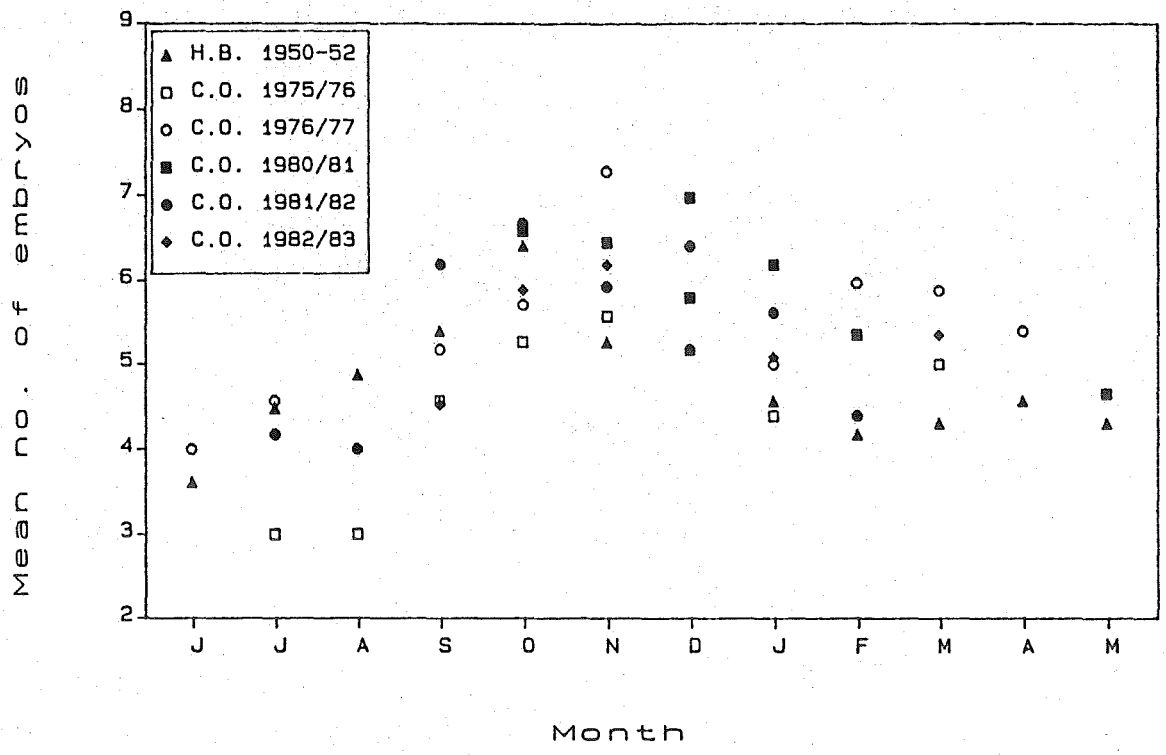

Figure 17.5 Seasonal variation in fertility levels indicated by the mean number of embryos per female for several breeding seasons in Central Otago (C.O.) and the period 1950-52 in Hawke's Bay (H.B.).

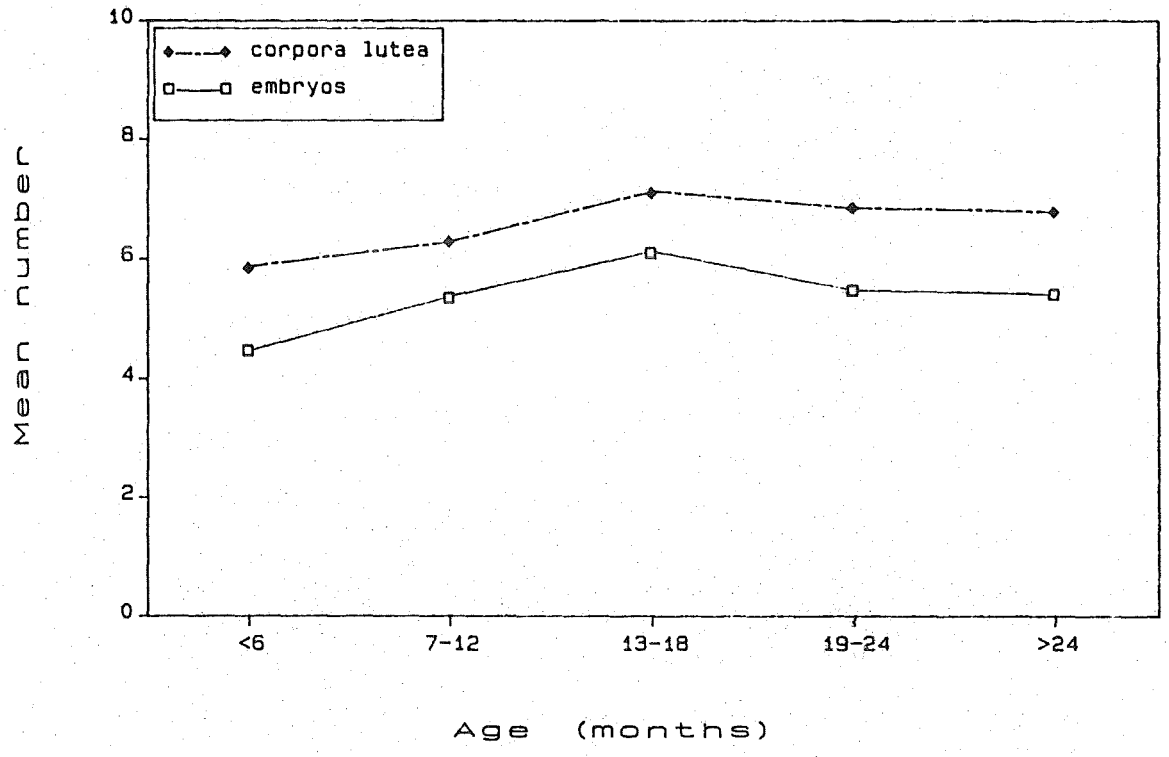

Figure 17.6 Variation in the mean number of corpora lutea and embryos per female with respect to age.

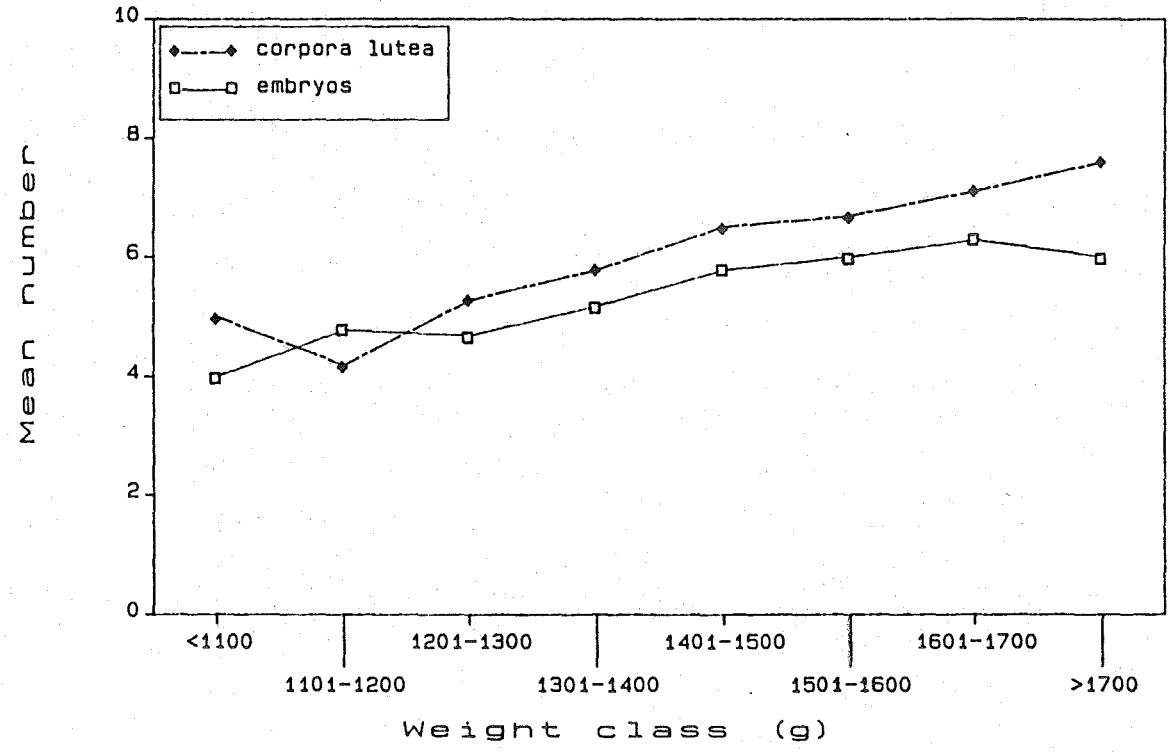

Figure 17.7 Variation in the mean number of corpora lutea and embryos per female with respect to carcass weight.

levels than lighter females (ANOVA, $F=8.53, p<.001$) (Figure 17.7). Condition, as indicated by Riney's abdominal fat index, was negatively correlated with the number of corpora lutea ($r=-0.17, p<.001$). Undoubtedly, seasonal variation in weight and fat-related condition influenced these relationships with female fertility. However, within individual months strong relationships between the number of corpora lutea and carcass weight and Riney's abdominal fat index still exist. The two months with the largest number of fertile females, November 1981 and September 1982, clearly illustrate these relationships. The influence of carcass weight was similar in both months, with higher fertility exhibited by heavier females ($p<.001$ in both cases). The relationship of fertility with Riney's abdominal fat index changed to a positive one, females in better condition having higher numbers of corpora lutea ($p=0.07$ for November 1981, $p<.05$ for September 1982).

Only two cases of superfertility were found among the 404 females examined. However, the incidence of this phenomenon is difficult to detect, as pre-natal mortality (see section 17.2.4) effectively reduces the chances of finding cases of polyovuly or polyembrony. Therefore, it is probably more common than indicated here (0.5%). Corpora lutea and embryo counts were not kept separate for the right and left ovaries and uteri respectively. Consequently, it was not possible to examine the data for cases of transperitoneal migration of ova, although this is known to occur in rabbits (Brambell 1944).

17.2.4 Pre-natal mortality

Pre-natal mortality can occur through failure of fertilised ova to implant and by the resorption of developing embryos during gestation. For convenience, these two sources of pre-natal mortality can be classified as 'loss of ova' and 'loss of embryos'.

Loss of ova can be estimated by comparing the ovulation rate (i.e. number of corpora lutea) with the number of embryos present for females during the

Table 17.4 Pre-natal mortality during the 1981/82 breeding season according to the stage of gestation.

Stage of gestation	Total litters	No. with loss	%	Total ova	No. ova lost	%
<11 days	25	17	68.0	178	25	14.0
11–15 "	7	5	71.4	51	10	19.6
16–20 "	29	23	79.3	237	58	24.3
21–25 "	39	29	74.4	281	56	19.9
>25 "	19	10	52.6	133	14	10.5
Total	119	84	70.6	880	163	18.5

early stages of gestation (Table 17.4). By restricting the comparison to the early stages of gestation, the amount of embryonic loss (between implantation and day 10 of gestation) that is attributed to pre-implantation loss is minimised. Loss of ova accounts for about 14% of the total number of ova ovulated. The majority of females (68%) examined at this stage (<11 days) exhibited some loss of ova.

Estimation of the level of embryonic loss is more difficult because some females may lose entire litters, effectively removing them from the data set. Because the data are cumulative, the loss at each stage also includes losses prior to that stage and there is some difficulty in apportioning the losses precisely. The highest levels of loss, both for the proportion of litters exhibiting loss and for the percent of ova lost, occur during the 16–20 day stage of gestation indicating that this is the peak period for the resorption of embryos. This is supported by information on the frequency of occurrence of resorbing embryos during each day of gestation (Figure 17.8). However, despite the low sample size (n=34), resorption was found at all stages of gestation. Uterine swellings that contained resorbing embryos were spindle-shaped, slightly wrinkled, and usually highly vascularised. In contrast, uterine swellings that contained healthy embryos were spherical, tumid, and clear in

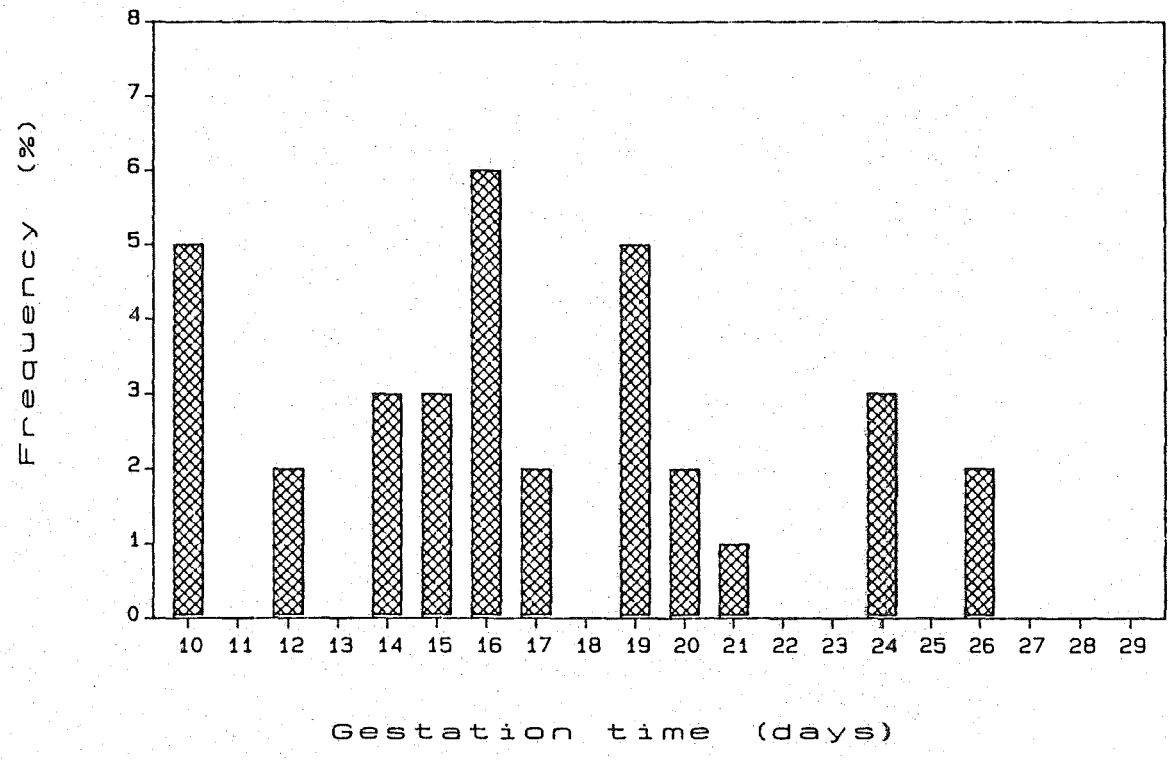

Figure 17.8 Frequency of resorption of embryos according to the stage of pregnancy.

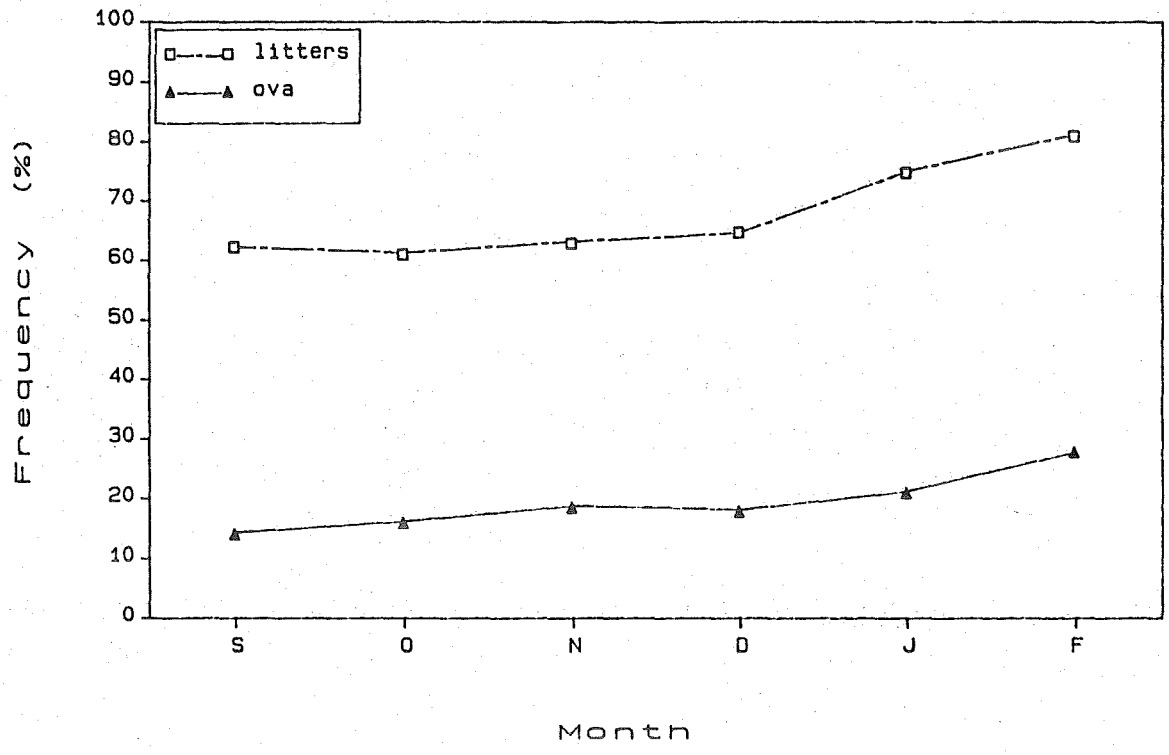

Figure 17.9 Proportion of litters showing some pre-natal mortality and the proportion of ova lost according to the stage of the breeding season.

appearance.

The decrease in the proportion of litters showing pre-natal mortality between the 16-20 day stage and later stages of gestation (see Table 17.4) suggests that some loss of entire litters is occurring. Using Watson's (1957) formula, the proportion of litters lost entirely can be estimated. This method assumes that most loss occurs before day 21 of gestation. It calculates the proportion of litters that survive (p) from the ratio of the proportion of litters without loss in the 11-15 day stage to the proportion of litters without loss in the 21+ day stages. For the 1981/82 breeding season:

$$p = \frac{(2/7)}{(19/58)}$$

Therefore, the proportion of litters lost entirely (1-p) was 12%.

The proportion of litters showing some pre-natal mortality is relatively constant (60-65%) for most of the breeding season but increases towards the end of the breeding season as young females begin to breed (Figure 17.9). The proportion of ova lost increases gradually throughout the breeding season, from about 15% in September to about 30% in February. The increase during the early part of the breeding season is probably partly due to the effects of a rise in female fertility. Pre-natal mortality was correlated with the initial size of the litter ($r=0.82, p<.001$); larger litters suffered greater percentage loss of ova compared with smaller litters.

Total pre-natal mortality (i.e. loss of ova and loss of embryos) varied according to the age and reproductive experience of the female (Table 17.5). Total pre-natal mortality was estimated as the difference between the mean number of ova ovulated and the mean number of embryos in the 21+ day stages of gestation. Females were classified intuitively into two groups, 'inexperienced' and 'experienced' breeders. This division was made on the basis of several factors including time of year, age of the female, and carcass weight. During the 1981/82 breeding season, pre-natal mortality for inexperienced females was 38.8% of the potential litter size, compared with

Table 17.5 Mean number of corpora lutea and embryos in the 21+ day stages for inexperienced and experienced females for the 1981/82 breeding season.

Month	Inexperienced		Experienced	
	Corpora lutea	Embryos	Corpora lutea	Embryos
Sep 81	6.43 (7)	5.25 (4)	8.29 (17)	6.67 (15)
Oct	-	-	8.11 (9)	6.57 (7)
Nov	9.00 (4)	1 (1)	7.24 (29)	6.85 (13)
Dec	6.75 (4)	3 (1)	8.00 (21)	6.67 (6)
Jan 82	6.00 (2)	5.00 (2)	7.10 (10)	5.38 (8)
Feb	5.73 (11)	3.57 (7)	7.40 (5)	7 (1)
Total	6.54 (28)	4.00 (15)	7.69 (91)	6.50 (50)

sample size in brackets

15.5% for experienced females. For the first five months of the 1982/83 breeding season pre-natal mortality was 22.9% and 15.7% for inexperienced and experienced females respectively.

The relationship between female fertility, pre-natal mortality, and age is not as simple as the above analysis suggests. In fact, pre-natal mortality increases again for females greater than 18 months old (Table 17.6). The variation with age is highly significant both for the number of corpora lutea (ANOVA, $F=4.93, p<.001$) and the number of embryos (ANOVA, $F=9.14, p<.001$). Although the proportion of pre-natal loss varies between females of different age classes, the actual number of ova or embryos lost is not significantly different (ANOVA, $F=0.45$, NS).

17.2.5 Productivity

Information on the frequency of pregnancy and the average litter size at birth enable estimates of productivity. Because of their low pregnancy rates, relatively low litter sizes, and high pre-natal mortality female rabbits less than six months old were excluded from this analysis. In any case their contribution to overall productivity would be minimal, as females less than

Table 17.6 Mean number of corpora lutea and embryos with an estimate of pre-natal mortality with respect to female age.

Age class (months)	Mean no. of corpora lutea	Mean no. of embryos	% loss
0–6	5.88 (26)	4.48 (46)	23.8
7–12	6.29 (104)	5.40 (139)	14.2
13–18	7.14 (95)	6.13 (130)	14.2
19–24	6.86 (42)	5.48 (54)	20.1
>24	6.81 (21)	5.41 (27)	20.6

sample size in brackets

six months old usually breed at times of the year when juvenile survival is low (Gibb et al. 1978).

Litter size at birth was calculated from litter sizes during the 21+ day stages of gestation. As shown in the previous section, pre-natal losses during the final stages of gestation are low, so this value should be close to the actual litter size at parturition. Frequency of pregnancy (F) was calculated from observed pregnancy rates according to the formula:

$$F = I \times (t/v)$$

where I = observed pregnancy rate,

t = duration of the sampling period, and

v = duration of visible pregnancy.

Productivity during any period is simply the product of the frequency of pregnancy and the average litter size for that period.

Continuous data were only available for the 1981/82 breeding season (Table 17.7) because autopsy sampling began after the start of the 1980/81 breeding season and no sample was obtained for February 1983. Based on the observed pregnancy rate (24.6%), the annual frequency of pregnancy for the period including the 1981/82 breeding season can be calculated as follows:

$$F = .246 \times (365/25)$$

$$= 3.59$$

Table 17.7 Observed pregnancy rates and estimated litter size at birth for female rabbits between June 1981 and May 1982.

Month	Number of Females	% visibly pregnant	Mean no. embryos >20 days
June 1981	48	0	-
July	52	9.6	5 (1)
August	102	1.0	-
September	57	59.7	6.45 (20)
October	21	47.6	6.57 (7)
November	62	56.5	6.00 (15)
December	33	72.7	6.67 (6)
January 1982	14	78.6	5.38 (8)
February	19	47.4	4.25 (4)
March	39	0	-
April	38	0	-
May	40	0	-
Total	523	24.6	6.07 (61)

sample size in brackets

Therefore, based on an average of 3.59 litters per year and an average litter size of 6.07, annual productivity for the period June 1981 to May 1982 was approximately 21.8 young per female.

Although no direct comparison with the previous or following breeding seasons was possible, three sets of data for the period October-January were available (Table 17.8). These values concentrate on the peak period for reproduction and cannot be extrapolated to estimate annual productivity. However, they are useful for comparing relative differences between years. Productivity appeared to be highest during the 1980/81 period, but similar for 1981/82 and 1982/83. Data from the latter periods illustrate the compensatory effect of frequency of pregnancy and litter size (see Table 17.8).

17.3 Discussion

The marked seasonality of breeding in Central Otago is in contrast to patterns found in other areas on New Zealand, including North Canterbury (Bell

Table 17.8 Frequency of pregnancy, average litter size, and productivity estimates for three consecutive October–January periods.

Period	Frequency of pregnancy	Average litter size	Productivity
Oct80–Jan81	3.74	7.20	26.9
Oct81–Jan82	3.08	6.16	19.0
Oct82–Jan83	3.82	5.50	21.0

1977), Wanganui (Williams and Robson 1985), and Wairarapa (Gibb et al. in press). In these areas the proportion of females pregnant throughout the year rarely falls below 20%. However, sharply defined breeding seasons also occur in parts of Western Australia (King et al. 1983), subalpine New South Wales (Myers 1971), southern Sweden (Andersson, Dahlback and Meurling 1979), Wales (Brambell 1944), southern France (Rogers 1979), and on Macquarie Island (Shipp et al. 1963, Skira 1978). These environments are characterised by either severe or strongly seasonal climatic conditions. Although it is improbable that the seasonal restrictions on breeding in all these areas are caused by the same set of factors, the overall influence of climate and its effect on the vegetation growing season seems to be the governing factor.

The duration of the breeding season in Central Otago was relatively constant and the timing of the onset of breeding varied only slightly between years. Rabbit populations in other stable environments with predictable climatic regimes exhibit similar reproductive features (Brambell 1944, Dunsmore 1974, Skira 1978). Small modifications in the timing of the onset of breeding are common (Lloyd 1963, Anderson, Borg and Meurling 1979) and these have been correlated with variation in weather conditions. In addition, less than favourable weather conditions may cause declines in pregnancy during the breeding season due to the failure of females to become pregnant at the post-partum oestrus (Brambell 1944). However, the varied origin of the autopsy samples in this study precludes a direct comparison of results. In parts of

Australia where climatic conditions, in particular rainfall, are unpredictable, there is much variation in the timing and duration of the breeding season (Stodart and Myers 1966, Myers 1971, Wood 1980). Presumably, the effect of rainfall on vegetation growth is the dominant factor in most environments. Out-of-season breeding in Central Otago was associated with higher than usual rainfall, although this was rare. The strong seasonality of factors influencing reproductive performance in Central Otago is confirmed by the very low levels of breeding between February and September.

Whatever factors are responsible for the rabbit's inherent reproductive pattern, it is generally acknowledged that the timing of the main breeding season is ultimately determined by the availability of an adequate food supply (Watson 1957, Poole 1960, Myers and Poole 1962, Shipp et al. 1963, Skira 1978, Andersson, Dahlback and Meurling 1979). However, variations in aspects such as the onset, duration, and productivity of the breeding season are produced by a complex set of environmental factors, acting differently in different environments (Lloyd 1970).

Unlike most monotocous species which vary little in terms of the period when pregnancies occur, polytocous post-partum oestrus breeders such as the rabbit exhibit considerable variation. Lagomorphs are induced ovulators (Asdell 1966) which serves to facilitate rapid reproductive responses to changes in environmental conditions. In fact, in some parts of Australia such as the arid areas of New South Wales the rabbit is completely opportunistic in its breeding pattern (Cooke 1970, Wood 1980). This ability to coordinate reproductive activity with favourable environmental conditions often accounts for the rabbit's success in marginal environments.

The sudden increase in the number of females pregnant at the start of the breeding season tends to indicate that the onset of breeding is influenced by some proximate factor, such as day length, which serves to coordinate reproductive activity within a population. Whether increasing or decreasing day length exerts a control is unclear for, in contrast to the Central Otago

pattern, the main peak of breeding in other areas of New Zealand begins before the winter solstice (Watson 1957, McIlwaine 1962, Bell 1977, Williams and Robson 1985). Andersson, Borg and Meurling (1979) suggested that in some instances weather conditions can act as a coordinating factor.

Whether the controlling influence which determines the exact timing of the onset of breeding is day length or some climatic variable such as temperature, an important relationship with latitude is evident as data from northern and southern hemisphere studies show (Figure 17.10). Populations at higher latitudes where climatic conditions exhibit greater seasonal variation and the environment is more severe begin to breed later than rabbits at lower latitudes. The influence of climatic factors on the food resource and individual metabolic requirements probably help to produce this pattern (McNab 1980). The termination of the breeding season is more variable and is probably influenced by a greater number of factors than the onset of breeding.

The annual (corrected) pregnancy rate in Central Otago (28% for 1981/82) is similar to that found in arid parts of New South Wales (Myers 1971) and northwestern Western Australia (King et al. 1983), but considerably lower than most other parts of Australia (Myers 1971) and New Zealand (Watson 1957, McIlwaine 1962, Bell 1977). Williams and Robson (1985) found an average of 61.7% of females visibly pregnant during a four year study of rabbits in the Wanganui region. In southern Sweden, where climatic conditions are similar to those in Central Otago, the annual pregnancy rate is about 31% (Andersson, Dahlback and Meurling 1979). Breeding in southern Sweden was similarly restricted to a main breeding season, unlike more stable northern hemisphere environments with higher rainfall (Lloyd 1970).

The youngest age at sexual maturity for rabbits in Central Otago (16 weeks) is similar to that recorded in other studies (e.g. Watson 1957, Myers 1971, Gibb et al. in press). Reproduction by young females is usually restricted to the final months of the breeding season and probably contributes little to overall productivity. However, when the breeding season is extended

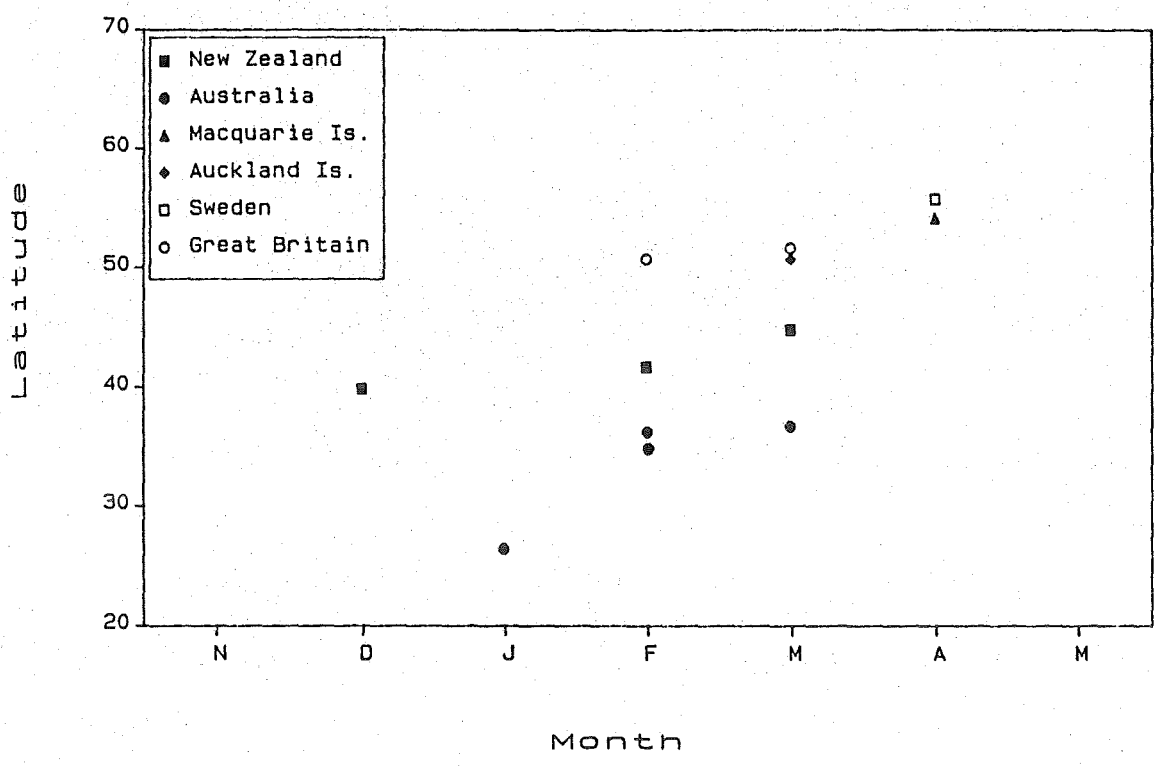

Figure 17.10 Relationship between latitude and the time of onset of the breeding season.

as occurred in 1982/83 the reproductive output of young females may be significant (Myers 1971).

A distinct cycle of male fertility occurred although some fertile males were found in all months. Both testis weight and testis position indicate that male fertility was highest in winter and spring, although in 1982 male fertility remained low during winter months. As previous research has demonstrated close relationships between spermatogenetic activity and either testis weight or testis position, it can reasonably be assumed that these indicators provide an accurate assessment of male fertility (Watson 1957, Myers and Poole 1962, Shipp et al. 1963, Skira 1978, Andersson, Dahlback and Meurling 1979). Most studies indicate that males become fertile at testis weights between 1.5 and 2.0 g. Sperm may be present at lower weights (Cooke 1974) but it is unlikely that sufficient quantities are available to ensure fertilisation (Brambell 1944). Male rabbits appeared to attain peak fertility between one and two years old.

Other studies have also shown that the increase in male fertility often precedes the breeding season by several months (e.g. Brambell 1944, Watson 1957, Bell 1977, King et al. 1983). The variation in the timing of the annual cycle of male fertility, not only between different areas but also between the 1981/82 and the 1982/83 breeding seasons, indicates that the pattern is largely determined by some variable environmental factor such as climate. Although Cooke (1974) demonstrated that male fertility was most closely correlated with day length, most studies show stronger relationships with climatic variables or the availability of food (Shipp et al. 1963, Rogers 1979, King et al. 1983, J T Martin unpub.). This, together with the fact that at least some fertile males are present all year round, confirms the opinion that the timing of the onset of breeding is a product of female fertility (Brambell 1944, Poole 1960, Myers and Poole 1962). However, the decline in male fertility seems to be quite closely correlated with the cessation of the breeding season.

Female fertility was subject to considerable variation according to the season and age of the female. Although fertility levels differed between the 1981/82 and 1982/83 breeding seasons, within each season the trends were similar. The seasonal pattern of female fertility (see Figure 17.5) was similar to that recorded in previous studies (Brambell 1944, Skira 1978, Andersson, Dahlback and Meurling 1979). As with males, female rabbits appeared to reach peak fertility between 13 and 18 months old, a feature previously noted by other workers (Myers 1971, Skira 1978, Gibb et al. in press). However, the subsequent decline in fertility for older age classes was not significant.

The positive relationship between fertility and carcass weight found by Brambell (1944) and Watson (1957) was confirmed. Although initially (when pooled) the data suggested that fertility was negatively correlated with the fat-related condition of the female, this trend was produced by the seasonal variation in fat levels. When individual monthly samples were examined separately it became apparent that adult females in better condition (i.e. with greater amounts of abdominal fat) had higher fertility levels.

Seasonal changes in ovary weight were more marked than those for testis weight, and mean monthly ovary weight provides a useful indicator of female fertility. However, ovary weight per se does not appear to influence female fertility as several females less than six months old were pregnant at very low paired ovary weights (100-200 mg). The youngest pregnant female (16 weeks old) had a paired ovary weight of only 103 mg. The reason for the significantly lower mean paired ovary weight in November 1982 is not clear, but the low number of adult females in the sample (n=7) may be partly responsible.

Pre-natal mortality accounted for 15-30% of all ova ovulated although this slightly underestimates the total pre-natal loss because some litters are lost entirely. As ovulation in the rabbit is dependent on copulation, the chance of losses due to ova remaining unfertilised must be insignificant.

Pre-implantation losses may be responsible for about 50% of all intra-uterine mortality, with the remainder due to resorption. Abortion of litters during the final stages of gestation probably occurs as in other polytocous mammals, but it is impossible to identify during autopsy. From the examples cited by Sadleir (1969), abortion in mammals appears to be a response to nutritional or density-related stress. As the rabbit is capable of resorption in response to these factors, thereby conserving part of its reproductive investment, abortion is probably infrequent. Total litter loss (12%) was considerably lower than found by Brambell (1942, 1944) in Wales (42-62%), Poole (1960) at two sites in Australia (39% and 58%), and McIlwaine (1962) in Hawke's Bay (47%). However, Watson (1957) calculated a loss of only 18% in Hawke's Bay and Myers (1971) has shown that total litter loss is very rare at several sites in Australia. The considerable variation in litter loss, not only between different environments but also within the same area at different times, suggests that a range of environmental factors combine to influence pre-natal mortality.

The distribution of resorbing embryos according to the stage of gestation was similar to that found previously (Brambell 1944, Lloyd 1963). While it appears from Lloyd's (1963) results and this study that the peak period of resorption is about day 16 of gestation, it probably occurs several days earlier (Brambell 1944). Brambell's sample size was larger and the distribution was smoother indicating that his results were more reliable.

Most litters exhibit some pre-natal mortality, with the highest losses occurring in the largest litters. Young females experienced greater pre-natal mortality than older females who had bred previously. This may occur because younger rabbits are usually subordinate and therefore experience greater stress (Mykytowycz 1960). The inclusion of young rabbits in the samples towards the end of the breeding season helps to explain the increase in pre-natal mortality (Brambell 1944, Skira 1978).

Throughout the breeding season most adult females became pregnant again at the post-partum oestrus. Combined with the relatively high litter size this allows the rabbit to reproduce at a rate close to its potential. Many species with high reproductive rates have few specific measures to counter predation and other mortality factors, and their high productivity is associated with low survival rates (Lloyd 1970).

Annual productivity was about 22 young per female, although there was evidence of some variation between different years. Table 17.9 compares litter size and productivity for Central Otago with results from other studies. There are some differences in the criteria used to calculate litter size and productivity; for example, some studies use the mean number of embryos as an estimate of litter size whereas others only include embryos greater than 20 days old in their calculations. Nevertheless, these figures provide a general indication of the variability of reproductive performance for the rabbit in a wide range of environments.

Compared with most other areas in New Zealand, productivity in Central Otago is relatively low despite the greater litter size. The difference in the length of the breeding season produces this result. The discrepancy between the two sets of results for North Canterbury is due to methodological differences. Bell (1977) calculated litter size and productivity for only that period of the year when the proportion of rabbits pregnant was greater than 50%, and did not correct for the initial stages of gestation when pregnancy is not visible. This method considerably underestimates the annual production of young and obscures comparisons with estimates of annual productivity. When Bell's data were used to calculate annual productivity, the result (approx. 42 young per female) was similar to Williams' (unpub.) estimate for the same area.

Myers' (1971) estimates for several different environments in Australia indicate considerably lower productivity than in most areas of New Zealand. However, Myers included all females greater than three months old in his

Table 17.9 Mean annual litter size and productivity for a number of different environments.

Location	Mean litter size	Productivity	Source
New Zealand			
Central Otago	6.07	21.8	present study
Hawke's Bay	5.03	18.1–21.5	Watson 1957
Wanganui	5.23	47.6	Williams & Robson 1985
Wairarapa	5.01–5.30	44.2–45.9	Gibb et al. in press
North Canterbury	5.54	29.4	Bell 1977
	5.85	37–43	J M Williams unpub.
Australia			
Subtropical	4.80	18.5	Myers 1971
Subalpine	4.53	13.1	Myers 1971
Arid	4.49	13.4	Myers 1971
Mediterranean	5.65	29.5	Myers 1971
Coastal	5.23	16.7	Myers 1971
Macquarie Island	5.63	19.3	Skira 1978
Great Britain			
Wales	4.87	10.4–11.7	Brambell 1944
	5.95	20.8	Lloyd 1963
England	4.36	–	Stephens 1952
	5.03	24.4	Mead-Briggs et al. 1975
Sweden	4.70	15.4	Andersson, Dahlback & Meurling 1979
France	4.70	18.8–23.5	Rogers 1979

calculations and did not allow for non-visible pregnancies. Gilbert and Myers (1981) subsequently recalculated productivity figures for these areas, correcting for pre-natal mortality and low pregnancy rates among young females. Their recalculated productivity estimates range from 15 young per adult (>9 months) female in the subalpine environment (Snowy Plains, NSW) to 38 young per female for the mediterranean environment (Urana, NSW). It appears that the subalpine environment restricts rabbit reproduction to a similar level to that in Central Otago. The mediterranean environment is similar to other parts of New Zealand with reproduction occurring during most months of the year (Myers 1971).

Northern hemisphere populations are characterised by generally smaller litter sizes, possibly a result of lower mean weights (Millar 1977, see also section 16.2.1). In addition, the low annual productivity of northern hemisphere populations indicates restricted breeding periods. The factors responsible differ between most areas, although they are generally correlated with climate (Andersson, Borg and Meurling 1979, Rogers 1979). In these environments low productivity combined with the generally high mortality rates probably limits the opportunity for density effects on reproduction as illustrated by Lloyd (1963, 1970). Central Otago rabbit populations are probably similar to northern hemisphere populations in this respect.

18 GENERAL DISCUSSION AND IMPLICATIONS FOR FUTURE CONTROL

18.1 Preamble

The main stimulus for this study was the increasing frequency of rabbit control operation failures in Central Otago. Very few 1080 poison operations result in greater than 70% kills (J Bell pers. comm.) and this leads to rapid resurgence of rabbit populations. About 50% of the area within the Alexandra Pest Destruction Board district is land with an 'extreme' or 'high' rating of rabbit proneness (Kerr et al. 1983). Much of this land has an inherently low productive capacity and rabbit control operations are heavily subsidised.

Rabbits have been present in high numbers in Central Otago since the late 1870's (Wodzicki 1950). Although densities were not high initially, they increased rapidly in association with the early settlers' management practices of burning and overstocking. Subsequently, the problems of desertification and loss of carrying capacity in Central Otago have been perceived as ones of high rabbit numbers only (Mather 1982). The role of fundamental land management practices in causing these problems in Central Otago was not addressed. The existence of semi-arid conditions facilitated the process of desertification and is just one of several factors, including rabbit numbers, which must be held responsible for the changes to the landscape.

Since the inception of large-scale poisoning operations for the control of rabbits in the 1950s, the apparent success rates of these operations has declined, especially in Central Otago where control is carried out annually in many areas. Rabbit Research Group (MAF) have examined a wide range of factors thought to be responsible for previous control operation 'failures', mostly associated with the methodology of poison control operations. Results of this research and the gradual elimination of technical causes of poison operation failures, have implicated rabbit behaviour as the most likely cause of continuing control operation failures. Similar research in Western Australia (Oliver et al. 1982) in response to the same problem also indicated that

rabbit behaviour was the most likely factor contributing to control failures.

The mechanism proposed as the cause of control failures is the selection for rabbits exhibiting neophobic behaviour (Bell 1979, Oliver et al. 1982). Similar changes have been demonstrated in rat populations subject to regular control measures (Boyle 1960, Jackson and Kaukeinen 1972). Other features of rabbit behaviour, notably social interactions, have also been shown to affect the results of control operations (Carrick 1956, Poole 1963b, Rowley 1963b). An essential prerequisite to the examination of behavioural effects during a poison operation was a detailed knowledge of rabbit behaviour in a population where as many individuals as possible were marked. This also provided the opportunity to compare rabbit behaviour in Central Otago with previous studies in Australia and Great Britain. Only one other study in New Zealand (Gibb et al. 1978) has included aspects of rabbit behaviour.

The desire for a more complete picture of rabbit biology in Central Otago and the need to relate behavioural and physiological features prompted the collection of regular samples of rabbits for autopsy.

The following sections on the biology of the rabbit in Central Otago and the existence of neophobia are limited to a discussion of the most important features. Detailed discussions of each aspect covered may be found in the preceding chapters.

18.2 Rabbit biology, in particular behaviour, in Central Otago

Rabbits on the Butchers Dam area are not typical warren dwellers. The nature of the habitat, especially the unsuitability of the substrate for burrowing, is reflected in the low incidence of active burrows. Most rabbits have their permanent resting locations in natural hollows beneath rocky outcrops; in some cases these hollows were extended by digging. Much of the habitat in Central Otago is similar to the Butchers Dam area so this situation is reasonably widespread.

Emergence from resting locations was more gradual and occurred earlier than found in Australia (e.g. Dunnet 1957b, Fullagar 1981). Similar findings were reported by Gibb et al. (1978) in the only other observational study of a New Zealand rabbit population. The greater diurnal activity of rabbits in New Zealand may be associated with the considerably lower number of predators in this country compared with Australia (see Table 6 in Soriguer and Rogers 1981).

In general, emergence occurred earlier in winter and spring, although daily emergence times were characterised by considerable variation. Seasonal patterns were strongly influenced by the level of food reserves as well as metabolic requirements. On the other hand, daily trends were influenced by weather conditions and, to a lesser extent, disturbances to the population. Temperature and wind direction were the most important climatic factors although, strictly, individual climatic factors should not be considered in isolation.

Feeding was the predominant activity during observation periods, comprising about 60% of all observations. The level and type of feeding behaviour varied in relation to the quantity and quality of vegetation available. Resting and grooming behaviour were the next most common forms of activity during the afternoon-early evening period. All other types of behaviour were relatively rare; social behaviour, an extremely important part of the rabbit's life history, made up of reproductive, territorial, aggressive, and displacement activities, comprised only 1-3% of all observations.

No major differences exist between the activity budgets recorded during this study and those found previously (e.g. Myers and Poole 1961, Gibb et al. 1978, Fullagar 1981). However, some minor variation is evident and this is probably associated with differences in observation times and experimental manipulation of the populations (e.g. enclosures, unnatural population densities) in these other studies.

Several individual activities appear to have been misclassified by other authors. Tail-flagging has been placed in the reproductive category by Southern (1948) and Thompson and Worden (1956). However, observations during this study indicate that tail-flagging is a territorial display (most commonly intrasexual). The similarity of the posture during this activity and several reproductive activities may have caused this confusion.

Two of the four displacement activities (scraping and hayraking) may be more appropriately classified within the aggressive category. Challenging was observed only once in two years so it is impossible to determine its correct classification. Only the paw-shake activity in an aggressive context conformed to the 'classical' definition of displacement behaviour (Tinbergen 1953, Marler and Hamilton 1966, Johnsgard 1967).

Social organisation exhibited similar variability to that recorded in several previous studies (e.g. Mykytowycz 1958, 1959, Myers and Poole 1959, Daly 1979) and is strongest during winter and spring. Although the level of social behaviour diminishes outside this period, some social group associations persist throughout the year. Outside winter and spring months there is less restriction to movement and social group boundaries either disappear or are only weakly defended.

The composition of social groups and the exclusiveness of their group territories varied not only seasonally but also between different parts of the study area. This variation may be explained by the concept of economic defendability of resources (Brown 1964, Harrison 1983) and reflected the heterogeneity of the habitat. In general, the 'best' areas were characterised by small social groups (2-4 rabbits) which defended their group territories vigorously. Poorer areas contained larger social groups (6-10 rabbits) with more extensive, but less well-defended, group territories.

Individual rabbits' activity ranges and movement patterns were similarly correlated with microhabitat features. In general, females had larger activity ranges than males, and dominant males sometimes had smaller activity ranges

than intermediate or subordinate males. These features are related to metabolic requirements (especially for female rabbits) and economic defendability. Most previous studies of range and movement patterns (e.g. Myers and Poole 1961, Gibb et al. 1978, Fullagar 1981) report markedly different patterns. However, Allen's (1939) study of cottontails in a heterogeneous habitat confirms the relationship between habitat quality and economic defendability.

The pattern of seasonal variation in activity range size is not clear, possibly because many factors including population density (Myers and Poole 1961), food quality (Gibb et al. 1978), and heterogeneity of the habitat interact to produce variation. The effect of population density was most noticeable following the poison operation in August 1982. The resulting decrease in population density caused an immediate expansion in the activity ranges of most rabbits.

Whereas activity ranges only represent a part of each rabbit's total home range, they cover most of the area utilised during the peak period of activity and are synonymous with the individual's feeding range. True home ranges for most rabbits at Butchers Dam comprised two core areas, one including the permanent resting location and the other around the point of peak activity. These core areas may be up to 100 m apart, depending upon the availability of permanent resting locations in relation to the feeding areas. Where burrowing is possible only a single core area is present but this was relatively uncommon on the Butchers Dam study area.

Shifts of activity range were rare among adult rabbits although small adjustments of range took place continually. Shifts of activity range were more frequent among young rabbits, especially males, probably reflecting pressure on juvenile rabbits to disperse. Data on marked rabbits observed outside the observation area confirm that most dispersal movements occur when rabbits are young. Movements of up to 1.5 km from the study area were recorded.

The most extensive and noticeable shifts of activity range for adult rabbits occurred following the poison operation in August 1982. Some rabbits that previously had not been seen for several months were observed on the study area only two days after the disappearance of rabbits killed during the poison operation. These changes indicated that adjustments of activity (or home) range can occur quickly in response to population density changes and suggest that olfactory signals of territorial 'possession' are relatively short-lived.

Although a mark-recapture (MRC) program was an essential part of this study, population estimates from MRC data vary considerably depending on what method is used. The best estimates of population fluctuations between successive sampling periods are provided by the Jolly-Seber method, and accuracy may be increased by including a non-capture component (i.e. observations of marked individuals) in the calculations. Long-term population estimates based on recapture frequencies also varied considerably depending on the method of analysis. The geometric method gave the best fit to the observed data and revealed a similar estimate of population size to that obtained from sight count data.

Much of the variation in both types of population estimates is produced by differences in trappability within the population. A number of factors influenced a rabbit's chances of being captured including season, age, and sex. In addition, considerable individual variation in trap response was evident. While MRC studies may have their uses, sight counts are considerably more accurate and less time-consuming for estimating the size of rabbit populations. This is especially true for Central Otago populations where habitat conditions are ideal for clear observations of relatively large areas.

Autopsy samples collected each month provided information on the age and sex structure, and reproductive characteristics of Central Otago rabbit populations, as well as on the growth and condition of rabbits within these populations. Results from this section confirmed the importance of environment

as an influence on various life history parameters and highlighted the adaptive qualities of the rabbit which facilitate its success in a wide range of environments.

The ageing technique using the dried weight of the crystalline eye lens was shown to be valid for ageing rabbits from Central Otago. Age structures of populations from this area characteristically contain large numbers of young rabbits and very few older individuals. This suggests high mortality and a rapid turnover rate, a reflection of the severity of environmental conditions especially during winter.

As in previous studies, rabbits less than six months old were under represented in the samples. Based on a liberal interpretation of population stationarity (Caughley 1977), a crude analysis of mortality was possible for rabbits older than six months. The mortality rate was about 0.3 per 3-month period although there was some evidence of an increase in mortality of adult rabbits associated with the second breeding season. Juvenile mortality is high in relation to adult mortality, but probably lower than for other parts of New Zealand because of better environmental conditions for juveniles during the breeding season.

Sex ratio differences range from an excess of females among juvenile age classes to an excess of males among older rabbits. However, it is unclear whether these differences are associated with differential mortality or sampling biases.

Growth and condition results reflect some measure of environmental conditions in Central Otago. A pause in growth is evident between about six and nine months of age where no increase in weight occurs. This corresponds to the winter period when the food supply is limited and metabolic requirements for maintenance are high. Adult male rabbits were heavier than female rabbits, except during summer months when the carcass weight of females was increased by the presence of mammary glands. Sexual dimorphism has not been recorded previously and is possibly a result of the greater size reached by rabbits in

Central Otago in comparison with other areas. Carcass weight data from a number of areas including Central Otago conform to Bergmann's rule, but major differences in size exist between rabbit populations in the northern and southern hemispheres.

Fat-related condition exhibits a strongly seasonal pattern; fat reserves are greatest during autumn and winter and lowest during spring and summer months. Fat reserves were highest when the food supply was poorest and environmental conditions were often severe. This suggests some form of hormonal control of fat reserves which appear to be related to metabolic requirements and physiological adaptation to the environment rather than the availability of resources to produce fat reserves. Flux (1971) demonstrated a similar pattern for hares in New Zealand. During the breeding season differences exist between males and females, the lower fat reserves for female rabbits reflecting the greater physiological stress imposed by pregnancy and lactation.

Although there is considerable seasonal and sexual variation in kidney weight, use of the kidney fat index (KFI) is not invalidated as has been found for cervids (Batcheler and Clarke 1970, Dauphine 1975). A high correlation between calculated KFI's and a visual estimate of fat reserves was demonstrated.

In contrast to other parts of New Zealand the breeding season for rabbits in Central Otago is sharply defined, a characteristic of populations in environments where conditions are severe or strongly seasonal. The main influence on the onset and duration of the breeding season is climate, through its effects on the food supply. Out-of-season breeding was generally associated with higher than usual rainfall, although this was rare.

Most breeding occurred between September and February although fertile males were found at all times of the year. This suggests that the onset of the breeding season is a product of female fertility. The youngest age at sexual maturity for both sexes was 16 weeks. Therefore, towards the end of the

breeding season reproduction by juvenile females may contribute to the total reproductive output of the population. However, pre-natal mortality was highest among young females in comparison with females who had bred previously. Although most litters exhibit some pre-natal mortality, overall pre-natal losses are lower in Central Otago populations than in other parts of New Zealand.

Annual productivity is about 22 young per female in Central Otago, lower than most other areas in New Zealand, reflecting the effect of the restricted breeding season. However, a relatively high litter size means that productivity is greater than for other strongly seasonal environments such as subalpine New South Wales (Myers 1971). Because of the seasonal restrictions on breeding, density-dependent effects on reproduction (Lloyd 1963, 1970) and population density (Myers and Poole 1963) are absent from Central Otago rabbit populations.

In summary, despite having age structures usually indicative of increasing populations, rabbit populations in Central Otago are relatively stable in contrast to the rabbit plagues and subsequent dramatic population crashes that occur in parts of Australia (Cooke 1981). The fat-related condition levels of adult rabbits suggests that populations are maintained below their potential peak levels by high mortality and a restricted breeding season. The opportunistic nature of the rabbit is reflected in the relatively high litter size, a strategy which increases productivity in an environment where the length of the breeding season is relatively short.

18.3 Neophobia and current poison control practices

Evidence from both poison trials and the golf ball experiment supports the hypothesis that previous control operations in Central Otago have selected for individuals exhibiting neophobic behaviour. Selection pressures appear to have been greatest where control measures are most intense. However, as the results of the Butchers Dam poison operation demonstrate, neophobic behaviour

does not disappear from a population in the absence of regular control operations; this confirms the genetic basis for this type of behaviour.

Neophobia does not describe a single, easily recognisable activity pattern but rather covers a continuum of avoidance responses towards unfamiliar objects. The range of responses is extremely varied although they all result in rabbits surviving poison control operations by failing to eat baits. At one end of the spectrum are rabbits which completely change their activity ranges to avoid all contact with the baits or furrow. In contrast, some rabbits exhibit no obvious adverse reactions to the unfamiliar objects and maintain their normal activity patterns during control operations. However, while they may be seen frequently in and around the furrow, they consistently fail to consume baits. Somewhere between these two extremes is the 'classical' neophobic response: this includes those rabbits that display a high degree of alertness when approaching the furrow and generally retreat to a 'safe' distance after close inspection of the furrow or baits. Repetitions of this 'classical' response were often observed over several days for the same rabbit.

While most bait-avoiders (i.e. neophobic rabbits) maintained constant response patterns over the duration of the poison operation, there was evidence that the 'degree' of the response diminished for some individuals. Several rabbits whose initial behaviour was best described by the 'classical' response eventually became indifferent to the furrow and baits after about two weeks. Nevertheless, they still failed to consume baits although the condition of the bait material may have been responsible for this failure. At the time that behaviour changes were noted the toxic baits had been in the field for about 72 hours so the possibility they had become unpalatable cannot be rejected. However, even if the baits were still appetising to rabbits by the time behaviour changes were occurring it is unlikely that increases in control success could have been achieved because of leaching of 1080 from baits caused by dew-fall. Current trials on the 1080 content of oat baits in Central Otago

indicate that under typical winter weather conditions (without rainfall) up to 75% of the 1080 content may be lost from baits in the first 72 hours (J Bell pers. comm.).

Evidence from both the Butchers Dam poison trial and the subsequent golf ball experiment confirmed the variable nature of neophobic responses within a population. Some results also suggest that the neophobic response may vary temporally within the same individual. While this suggests that the mechanism responsible for the selection of neophobic behaviour in rabbits does not conform strictly to Krebs and Davies' (1981) definition of an evolutionary stable strategy, assessment of the relative importance of genotype and environment can only be speculative. If such an interaction of factors does occur, there are important implications for scheduling control operations to coincide with conditions under which rabbits are least likely to be disposed towards neophobic behaviour (i.e. under conditions of food stress).

Effects of disturbance associated with the poison operations were evident especially in causing delays to emergence on the days the baits were laid. These reactions declined on subsequent days with emergence patterns returning to normal for most of the duration of the poison operation. Disturbance effects are unlikely to contribute to poor success rates of control operations, especially aerial operations where disturbance is minimal.

Social behaviour effects were observed in both poison experiments. Dominant rabbits were frequently observed chasing other rabbits from the bait lines or furrow. However, in each case the presence of excess baits afforded all rabbits the opportunity to consume baits. Where bait distribution is poor or bait is laid sparingly, social behaviour could affect the success rate of a control operation.

18.4 Future control options and strategies

A number of alternatives to the standard practice of control using 1080 poison are available. These alternatives vary in their cost and potential

effectiveness but need to be considered if increases in control success are to be achieved. Included among these alternatives are new poisons and baits, reintroduction of the viral disease myxomatosis, recommercialisation of the rabbit, and changes in land use. Some of the advantages and disadvantages associated with each of these options are discussed below.

The introduction of alternative poisons, notably anticoagulants such as brodifacoum, has been examined on a trial basis. Preliminary results suggest that control success is no greater than typical 1080 control operations (J M Williams pers. comm.). However, a significant advantage of anticoagulant poisons is that they require only a single application, thereby eliminating the substantial costs of prefeeding. Some information on secondary poisoning of non-target species (principally predators) indicates that the risks associated with brodifacoum are no greater than for 1080 but this aspect requires further study.

Development of new baits has also received some attention in recent years. These baits are based on pollard and are produced in standard-sized pellet form. Initial trials suggest that acceptance of pollard-based baits is similar to carrot and oat baits, although anecdotal evidence of changes in the relative acceptance of carrot and oat baits at different times of the year is common. The main advantages of manufactured baits are that the poison can be added at the point of manufacture thereby reducing the possibility of variation in toxic loading, and that manufactured pellet baits persist in a palatable form for longer than carrot baits under most conditions (pers. obs.).

Since about 1980 the pressure from the farming sector for the reintroduction of the viral disease myxomatosis has increased substantially. Reductions in government funding of the pest destruction industry have added impetus to this movement. Diametrically opposed to those in favour of myxomatosis is a vociferous public lobby whose opposition is based mainly on animal welfare grounds.

While it is almost certain that myxomatosis would result in a substantial reduction in rabbit numbers initially, several important factors must be taken into account if its introduction is to be considered seriously. The rabbit problem is restricted to a relatively small area of New Zealand (principally Central Otago); there is no possibility that myxomatosis could ever be restricted to this area. Therefore, it is inevitable that myxomatosis would spread throughout New Zealand. The presence of a disease with visible symptoms in our rabbit populations would probably significantly reduce the amount of recreational hunting that occurs and eliminate any chance of recommercialisation of the rabbit for its meat. Any reduction of rabbit populations, especially low density populations, would result initially in some prey switching by predators such as feral cats and ferrets. Although predator populations might eventually stabilise at lower levels, the immediate impact on native fauna, especially bird species, would be detrimental.

Effects on the pest destruction industry of the introduction of myxomatosis would depend largely on the long-term perception of the rabbit problem by the farming sector. During the early years of myxomatosis with high kills and good control, the continued existence of pest boards in their present form may be hard to justify. The employment-related problems arising from a destabilisation of the pest destruction industry and the social consequences in rural areas could be considerable.

Another disadvantage associated with myxomatosis is the possible role of the rabbit as a carrier of the foot-and-mouth virus (White 1983). The risk of spread of a foot-and-mouth outbreak could be greatly increased by the presence of the rabbit flea and containment of the disease might be more difficult.

Leaving aside the considerable emotional public opposition to myxomatosis, several strong reasons against its introduction are evident. Although it cannot be discounted as a possible alternative control technique, it would be prudent to exhaust all other possibilities before a decision to introduce myxomatosis is made. Myxomatosis represents a permanent and

irreversible change and should not be entered into hastily.

The viability of the recommercialisation of the rabbit for its meat and fur is uncertain. However, this aspect certainly deserves investigation. Possum populations can be maintained at relatively low levels within localised areas by intensive commercial trapping and poisoning by private operators (B Warburton NZFS pers. comm.). Depending on the market trends for meat and fur, private operators may be able to reduce rabbit densities in some areas, particularly high density areas such as Central Otago. Undoubtedly problems of administration and access to property would exist but these should not be insurmountable. It is conceivable that the existing pest board structure could be used to administer such a system.

The question of changes in land use in rabbit-prone areas has not been adequately examined. Afforestation or retirement of problem areas may offer a viable alternative for the worst affected land. On a economic basis it is difficult to justify current levels of control on land with a high rating of rabbit-proneness. Such land is characteristically of marginal economic value and the added productivity resulting from rabbit control is generally outweighed by the costs of control (Kerr et al. 1983). One possible consequence of increased control of rabbit populations (as may result from the reintroduction of myxomatosis) is a change in the nature of the habitat. This could include a magnification of the weed problem, potentially a far more expensive scenario than the current rabbit problem.

18.3 Conclusions

Historically, the perception of the problem of desertification and low productivity of many areas in Central Otago has been regarded as a 'rabbit problem'. Rabbits are only one factor contributing to this situation; poor land management practices including overstocking and the indiscriminant use of fire played the primary role in the origin of the problem. Unfortunately, the historical perspective still pervades the current view of the problem.

Future research must concentrate on an economic basis for control; where the benefits of control do not outweigh the costs, alternative options for land use should be considered. Myxomatosis should only be regarded as a last resort; all other alternatives which offer some possibility of relief from the 'rabbit problem' should be exhausted before a decision on myxomatosis is made.

Rabbit populations in Central Otago exhibit many similarities with populations in other areas, notably subalpine New South Wales in Australia and its mediterranean homeland. However, some features of rabbit biology including population age structures and reproductive characteristics vary quite markedly from those found in other areas of New Zealand. This demonstrates the controlling influence of environment and highlights the rabbit's opportunistic nature and its ability to adjust to geographically and temporally varied conditions. Behaviour probably exhibits the least variability of all aspects of rabbit biology, as evidenced by the similarity of results obtained during this study to previous studies in Great Britain and Australia.

One aspect of behaviour that has changed radically, however, is that associated with control operations. Rabbits exhibiting neophobic responses towards unfamiliar objects have been selected for and this has led to the current situation of poison control failures in areas where control operations have been carried out regularly in the past (notably Central Otago and parts of Western Australia). Under present control methodology there is little scope for improvement in poison control success rates. It is ironic, but nevertheless inevitable, that each successive poison control operation reduces the potential success of future operations.

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APPENDIX 1

Brief descriptions of the 53 behaviours recognised during observations on rabbits at Butchers Dam.

MISCELLANEOUS:

1 Entering	Moving into and out of sight down a burrow.
2 Emerging	Appearing at the burrow entrance.
3 Looking down	Stationary posture, usually brief, and often with head just inside the burrow entrance.
4 Digging	Specific to digging of burrows, including not only the actual digging movements but also the shifting of loose earth from the burrow and its surrounds.
5 Defecating	
6 Urinating	

FEEDING:

7 Grazing	Close-cropping of short vegetation with frequent pauses to scan the surrounding area. Often rabbits graze a semicircle while remaining in one position.
8 Browsing	Feeding on taller vegetation, often necessitating stretching or standing on the hind legs to reach the food source.
9 Scratch feeding	Scraping earth away from the base of plants in order to eat the roots.
11 Coprophagy	Reingestion of faeces directly from the anus.

GROOMING:

15 Scratching	Scratching movements with the fore or hind paws at parts of the body.
16 Washing	Licking the paws or parts of the body. The fore paws are often licked and then used to rub the head and neck regions.
17 Shaking	An abrupt shake of the whole body, usually while in a rigid stance on all fours.
18 Mutual grooming	Licking the head or body of another individual.
24 Stretching	Arching of the body dorsally and/or ventrally, often accompanied by yawning.
25 Yawning	
26 Rolling	Rolling and rubbing the whole body against the ground.

RESTING:

20 Sitting	Upright sitting posture, with the weight on the hindquarters and the extended fore legs. Ears may be erect or laid flat along the back.
21 Squatting	Resting posture with both pairs of legs folded under the body. Ears usually laid along the back.
22 Lying	Resting with the body flat on the ground, sometimes partly on one side, legs outstretched to the same or different sides.
23 Basking	Body flat against the ground but with legs stretched out directly backwards and forwards along the midline.

LOCOMOTORY:

28 Lope	A slow, relaxed but steady gait composed of a series of hops.
29 Run	A quicker form of movement, but not as rapid as that when fleeing (34) from danger.
30 Skit	An erratic series of movements, usually by young rabbits, lacking any definite directional orientation. Often includes somersaults and twists in mid-air.

ALERT:

31 Upright	Resting on the hindquarters with the body held in an erect stance, sometimes stretched up to its fullest height. Ears forward and erect, nose sniffing and fixed gaze usually in the direction of the disturbance which elicited this posture.
32 Crouch	Tense posture, similar to squatting, but with the body held slightly off the ground. Ears usually erect and gaze fixed.
33 Thump	Ground struck with both rear paws simultaneously, always when the rabbit is in a crouched position, usually following the detection of danger.
34 Fleeing	Rapid escape reaction with the rabbit running at full speed, often towards a burrow or some other form of cover.

REPRODUCTIVE:

36 Inspects	Approach and sniffing of another rabbit, usually a female, possibly for olfactory clues.
37 Inspected	
38 Follows	Loping after another rabbit, seldom more than 1–2 m behind, usually done by males to females.
39 Followed	
40 Circling	Loping around a stationary rabbit (female), often with frequent changes of direction.
41 Circled	Female rabbit in a squatting position, usually with the ears laid flat. Sometimes the female continually reorientates herself so the male never gets behind her.
42 Enurinates	Usually an intersexual display, where one rabbit (the male) either twists towards or jumps over another (the female) and ejects a squirt of urine at her.
43 Enurinated	The female is usually in the squatting posture when this occurs but may be feeding. In some cases there is no reaction to enurination but at other times the recipient will shake its body for several seconds, often as a prelude to grooming.
44 Nuzzles	Pressing of the head against the head or body of another rabbit, with a rubbing motion.
45 Nuzzzled	
47 Copulation attempt	The act of mounting a female by a male with his fore paws resting on her back or shoulders, usually unsuccessful and often at the wrong end!
48 Mounted	

49 Copulation	Rarely lasts for more than several seconds, with 5-10 rapid thrusts before the male falls to one side of the female. May be repeated several times over a short period of time (1-2 minutes).
TERRITORIAL:	
46 Tail-flagging	Most commonly an intrasexual display, where two individuals parade backwards and forwards along an imaginary boundary with exaggerated, stiff loping gaits. The tail is held erect over the rump and is usually curved to one side.
53 Chinning	Pressing or rubbing the chin against the ground (often around a burrow entrance) or vegetation, so that secretions from the chin gland are left on the object.
54 Patrolling	Loping with a stiff gait over its normal range while gazing around in all directions. Frequent pauses during this activity often include the individual assuming an upright stance.
AGGRESSIVE:	
55 Threat	An aggressive approach towards another rabbit which causes it to move away, with the first rabbit usually stopping at the point previously occupied.
56 Move away	The result of an aggressive approach by another rabbit.
57 Chase	Most commonly intrasexual, this can result from a threat or sometimes when one rabbit ventures too close to another. Performed at a run, it may last only several seconds or can take much longer with both rabbits covering a considerable distance.
58 Chased	
61 Fighting	Close physical combat, rarely exceeding several seconds, between two rabbits which jump up and at each other striking out with their hind legs.
DISPLACEMENT:	
62 Scraping	Violent scratching at the ground with the fore paws, sometimes with the gaze fixed on another rabbit.
63 Pawshake	Resting on the hindquarters while shaking the fore paws.
64 Hayraking	Similar to scraping, but where the fore paws rake up considerable quantities of vegetation.
65 Challenging	An aggressive approach towards another individual where the object of the aggression cannot be reached. This was observed between individuals on opposite sides of a fence line and often accompanied by other forms of displacement behaviour.

APPENDIX 2

Daily bait counts from each of the 5 m count plots, for each of the prefeeds and the poison feed.

Plot	Day (August-) 10	11	12	13	14	15	16	16	17	18	19	20	20	21	22	23	24	25
Furrow and baits:																		
E8	102	99	98	69	30	2	0	113	96	34	0	0	105	93	85	75	80	75
C6	107	101	91	61	12	0	0	126	71	18	2	0	115	101	95	83	83	82
E5	121	118	109	102	78	1	0	134	55	20	0	0	102	54	53	35	36	32
I6	112	111	89	89	49	0	0	117	77	10	0	0	90	37	37	37	35	35
KL8	118	108	95	76	58	0	0	112	84	46	1	0	152	72	66	59	57	57
M6	106	106	102	85	70	0	0	119	88	34	0	0	105	82	82	67	64	62
N7	128	117	110	68	21	0	0	109	40	6	0	0	100	89	79	76	75	75
M10	136	136	120	120	111	40	0	127	108	29	1	1	115	103	77	75	67	68
K11	121	105	103	78	73	7	0	108	93	57	0	0	107	71	64	61	64	64
I10	104	104	102	95	84	8	0	112	63	21	1	0	75	60	52	54	52	52
Baits without furrow:																		
F7	139	137	127	98	20	0	0	134	55	20	0	0	107	82	80	70	67	65
K9	134	126	126	123	52	9	0	123	63	42	0	0	60	37	35	36	36	36
A5	-	134	68	20	0	0	0	132	41	5	0	0	119	64	64	58	57	57
P6	-	120	106	22	1	0	0	121	75	3	0	0	122	25	27	26	26	26

APPENDIX 3

The following paper appears in the New Zealand Journal of Zoology, Volume 12, Part 2 (1985).

EFFECT OF STORAGE IN FORMALIN ON ORGAN WEIGHTS OF RABBITS

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Abstract The changes in weight of liver, kidneys, perirenal fat, adrenals, ovaries, and testes from a sample of 37 rabbits, **Oryctolagus cuniculus** (L.), following storage for up to 128 days in 10% formalin are described. The greatest changes caused by preservation occur in the first 24 h, but continue at a decreasing rate until by Day 32 only minor differences were found between successive weighings. In a large volume of formalin all tissue maintained greater weight than similar tissue stored in a small volume. Correction factors are necessary to estimate initial weights from material preserved in 10% formalin.

Keywords **Oryctolagus cuniculus**; formalin; fixation; tissue storage; organ weights

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INTRODUCTION

Many autopsy studies on wildlife involve the collection and preservation of material in the field for later measurement in the laboratory. Commonly used fixatives, such as formalin and ethyl alcohol, affect tissues both physically and chemically (Pearse 1968; Kiernan 1981). Previous work on fish has revealed that considerable changes in length and weight follow fixation in formalin (Parker 1963; Stobo 1972; Cadwallader 1974). However, for wild mammals, only the effects of formalin on the weight of the eye lens, an age indicator, have been assessed (Lord 1959; Friend 1967). Although previous workers have frequently preserved organs and tissue samples for later measurement, there appears to be no information on the quantitative changes in whole organs during fixation.

If weight changes in tissue samples are known, correction factors can be applied to preserved material to estimate initial or fresh weight. The different biochemical compositions of various tissues, strength and volume of fixative, and length of time the material is stored, could all produce weight changes.

This paper describes the weight changes of liver, kidneys, perirenal fat, adrenals, ovaries, and testes of the European rabbit, **Oryctolagus cuniculus** (L.), following various lengths of time in 10% formalin. The most likely histological factors that produce the observed changes are discussed, and correction factors are provided to estimate initial (i.e. pre-preservation) weight.

MATERIALS AND METHODS

Thirty-seven rabbits were collected after a control operation using 1080 (sodium monofluoroacetate) poison in Central Otago, New Zealand. The carcasses were put into 2 polythene bags to prevent dehydration, and then frozen for several days before transportation to the laboratory. After thawing, the liver, adrenals, and reproductive organs were removed and stripped of

associated fat. Kidneys were removed with surrounding fat left intact, before the perirenal fat was removed following the technique of Riney (1955).

Before preservation, all material was weighed on a Mettler PC440 pan balance. Liver weight was recorded to the nearest 0.1 g, kidneys, perirenal fat, and testes to 0.01 g, and ovaries and adrenals to 0.001 g. The material was then immersed in 10% formalin (4% solution of unbuffered formaldehyde in fresh water). The liver (weighing 35–60 g) and left organs plus perirenal fat (weighing 7–10 g) were stored in 150 ml of formalin. The right organs and fat (7–10 g) were stored in 50 ml of formalin. The material was weighed after 1, 2, 4, 8, 16, 32, 64, and 128 days, after the organ or fat deposit had been lightly rolled on absorbent paper to remove surface liquid.

To determine the accuracy of the procedure, 1 set of material at 64 days was weighed 10 times in 60 min. The material was returned to the formalin after each weighing. The 10 consecutive measurements show that coefficients of variation are greatest for the smallest organs weighed, the adrenals and ovaries (Table 1). Kidneys, testes, and liver all have coefficients of variation less than 1%. Compared to material of a similar weight the variability in perirenal fat measurement is quite high.

Table 1 Mean values and variability of measurements obtained from 10 consecutive weighings of preserved material following a standardised method of removal of surface liquid.

Organ	Mean wt. (g)	Standard deviation	95% Conf. limits	Coeff. of variation
Liver	38.1	0.3	0.2	0.66
Left kidney	5.35	0.012	0.009	0.22
Right kidney	6.47	0.016	0.012	0.25
Left perirenal fat	1.65	0.034	0.026	2.06
Right perirenal fat	2.48	0.059	0.044	2.35
Left adrenal	0.051	0.011	0.009	2.23
Right adrenal	0.052	0.019	0.014	3.69
Left ovary	0.047	0.009	0.007	1.88
Right ovary	0.029	0.009	0.006	2.98
Left testis	1.17	0.005	0.004	0.41
Right testis	1.14	0.007	0.005	0.61

Table 2 Mean percentage of initial weight of various organs with time in 10% formalin, with 95% confidence limits. n = number of organs.

Organ	n	Days in formalin 1	2	4	8	16	32	64	128
Liver	37	97.61±1.13	95.34±1.28	94.96±3.47	91.97±1.34	90.63±1.44	89.64±1.59	88.29±1.57	87.68±1.46
Rt kidney	37	101.56±0.72	100.35±0.69	99.48±0.72	98.56±0.66	97.72±0.64	97.45±0.79	96.52±1.24	97.09±0.93
Rt perirenal fat	37	114.25±2.17	114.15±3.08	110.75±3.43	111.45±3.88	109.50±2.87	109.89±2.54	106.56±2.37	108.08±2.55
Rt adrenal	27	102.32±3.14	99.31±2.00	99.09±1.82	99.34±3.01	98.27±1.85	100.18±2.10	100.07±1.99	100.61±2.92
Rt ovary	14	106.34±4.34	106.37±4.44	105.54±4.82	102.48±5.64	104.80±2.77	103.19±4.50	101.93±4.64	102.80±4.31
Rt testis	23	100.94±0.95	100.76±0.90	100.25±0.79	101.84±4.18	99.50±0.92	99.72±0.88	99.64±0.96	99.60±0.82

RESULTS

The relative weight changes for the liver, right organs, and perirenal fat over time spent in formalin, are presented in Table 2 and Fig. 1. Damage during autopsy reduced the number of right adrenal glands available to 27. Apart from reproductive organs, the other results include data from all 37 rabbits autopsied. Correction factors have been calculated for all the material examined, to determine initial weight as follows:

Initial weight (g) = Preserved weight (g) x Correction factor

Correction factors for storage periods of 32, 64, and 128 days are presented in Table 3, together with an average correction factor.

Noticeable differences existed in weight changes between the left and right organs and fat deposits, although the direction of weight change was similar to that of the kidney and perirenal fat (Fig. 2, 3). The right organs were always significantly heavier compared to their initial weights than the left organs.

Table 3 Correction factors to estimate initial weight for material preserved in 10% formalin. n = no. of organs.

Organ	n	Days in formalin 32	64	128	Av. correction factor
Liver	37	1.116	1.133	1.141	1.130
Rt kidney	37	1.026	1.036	1.030	1.031
Rt perirenal fat	37	0.910	0.938	0.925	0.924
Rt adrenal	27	0.998	0.999	0.994	0.997
Rt ovary	14	0.969	0.981	0.973	0.974
Rt testis	23	1.003	1.004	1.004	1.004

DISCUSSION

The narrow confidence limits for all tissue types examined (Table 1), indicate that the drying and weighing method used gives reproducible results. Removal of variable amounts of surface liquid before weighing probably caused

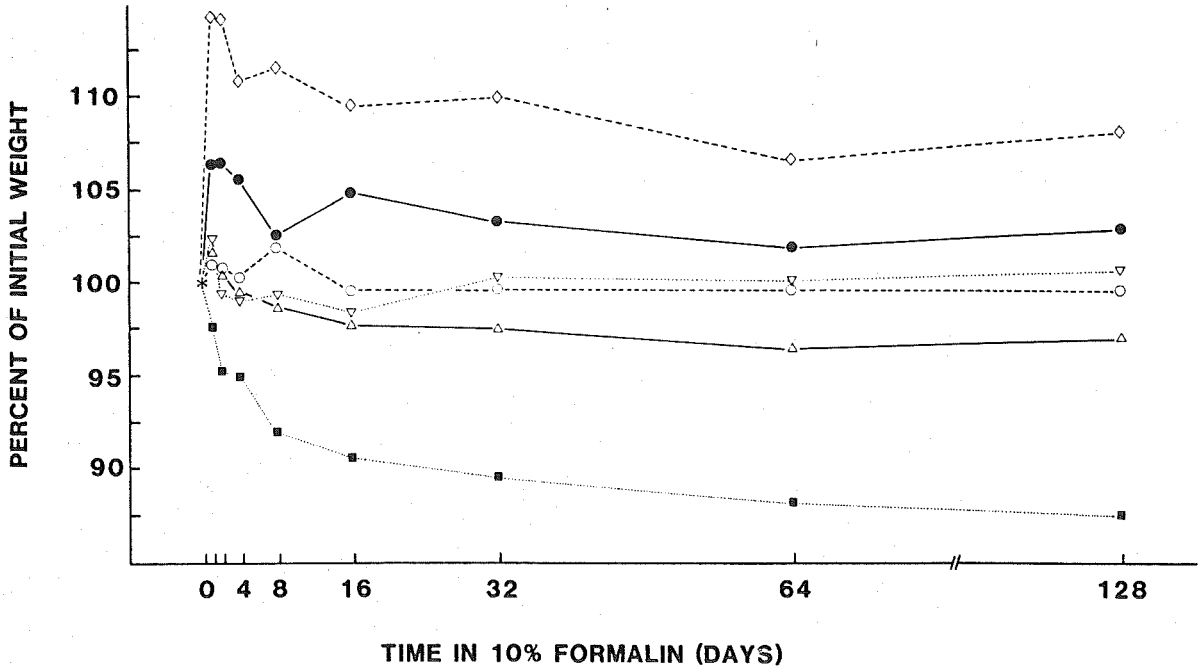

Fig. 1 Relative weight changes for the liver ▪, right kidney △, perirenal fat ◇, adrenal gland ▽, ovary ●, and testis ○, after storage for various lengths of time in 10% formalin (* = initial weight for all organs).

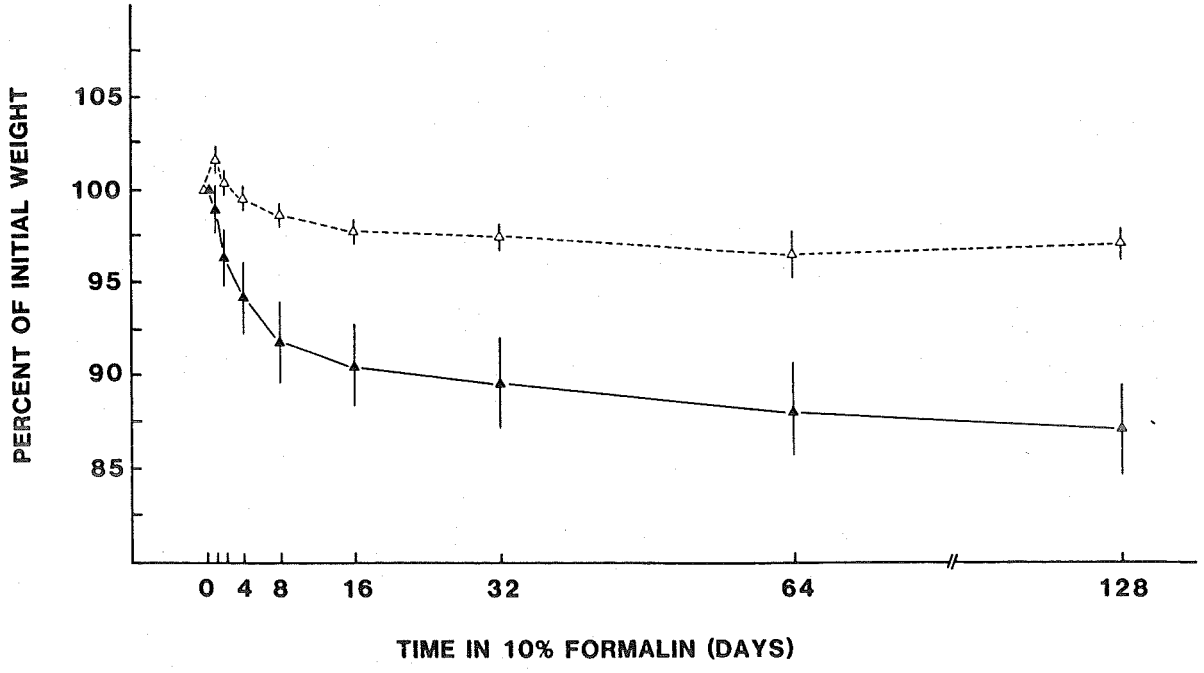

Fig. 2 Weight changes occurring to the left ▲ and right △ kidneys (mean ± 95% confidence limits), following preservation in 10% formalin for various lengths of time.

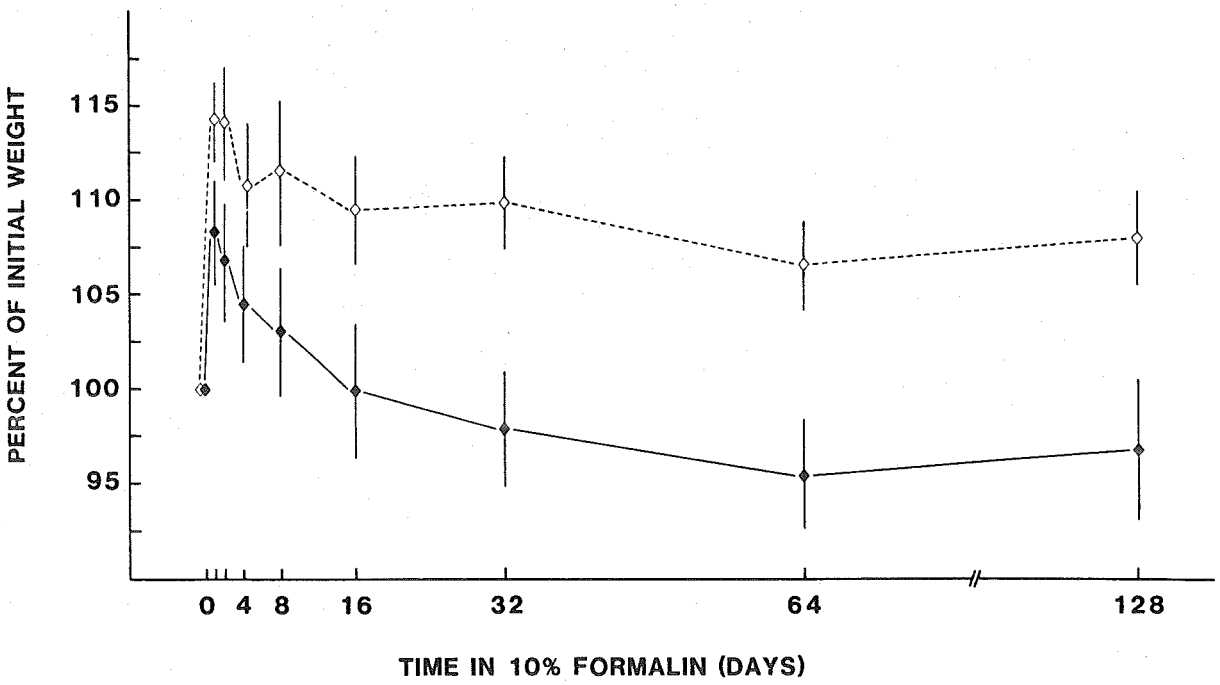

Fig. 3 Weight changes occurring to the left ♦ and right ◇ perirenal fat (mean ± 95% confidence limits), following preservation in 10% formalin for various lengths of time.

most of the measurement error. Large organs showed less variablility in measurement than small ones, also contributing to error. However, perirenal fat showed relatively high variability; possibly because of its irregular shape making removal of surface liquid difficult. Other organs except for the liver had no folds or involutions to retain surface liquid. This difference in shape may explain why the coefficient of variation for liver weight is slightly higher than for the lighter, but more regularly shaped, kidneys.

The greatest weight changes in formalin occurred during the first 24 h, although the direction of the change varied between the material (Fig. 1). Subsequently, the rate of weight change declined until differences between consecutive weighings were insignificant. Right perirenal fat and ovary weights increased markedly at first, but then declined to a level much closer to their initial weights. Conversely, liver weight immediately declined, eventually stabilising at 87% of its initial weight. Although preceded by a small increase in the first 24 h, right kidney weight followed a similar pattern of decline to the liver, eventually reaching a stable value at 97% of its initial weight. The trend in weight change for the right adrenal gland did not conform to either of these patterns. After an initial increase over the first 24 h, adrenal weight decreased to a minimum after 16 days, but then rose until almost identical with the original weight. Right testis weight increased slightly, followed by a small decrease, but never deviated much from the initial weight.

The variation in weight is so great up to 16 days that any correction factors should be avoided. Most of the material examined exhibited only minor changes after the Day 32 weighing. As formalin has one of the slowest fixation rates of any fixative (Culling 1974; Kiernan 1981), it is not unexpected that changes were still occurring up to Day 32.

The weight changes observed are the result of a complex set of factors and cannot be explained by osmotic action alone. Particularly important in the initial stages are the tonicity of the dilutant and the tissue fluids,

membrane permeability, Donnan equilibria, and inability of the cells to continue active osmotic work (Bahr et al. 1957). Over a longer period, slow chemical changes may also have an effect. The increases in weight observed for perirenal fat, ovaries, and adrenals suggest that the tissues are initially hypertonic. However, 10% formalin has an osmotic pressure of about 32 atmospheres (almost 5 times that of mammalian blood). Therefore, the observed weight change is the reverse of what would be expected on the basis of osmotic pressure. Young (1935) has shown, however, that some fixatives, including formaldehyde, require the presence of a balanced salt to give an osmotic pressure similar to that of the tissue. When fresh water is used instead of a saline solution, vacuolation and swelling of the cells occurs, as if the tissue were hypertonic. This is probably because of the minimal osmotic effect exerted by the formaldehyde, as it has a very low molecular weight and is therefore very permeable. Consequently both fixative and dilutant penetrate rapidly into the tissue, causing an increase in volume.

The subsequent decline in weight probably reflects shrinkage of the whole tissue (i.e. loss of tissue fluids) brought about by cross-linking of protein molecules, a reaction which requires several weeks for completion (Hopwood 1969; Kiernan 1981). This helps explain why marked weight changes continued up to Day 32. Weight loss could also result from breakdown and extraction of relatively dense tissue components such as proteins or glycogen. Bahr et al. (1957) noted that, although individual data varied greatly, most previous investigations have revealed that fixation in formaldehyde caused tissue samples to swell followed by a gradual decrease in volume and weight.

Some of the weight loss for perirenal fat deposits after the first 24 h could be attributable to cell membrane rupture and subsequent release of cellular contents, here mostly lipids. This was confirmed by the appearance appearance of fat globules on the surface of the formalin by Day 16 or Day 32 in most containers. Cells rupture because of an increase in volume of their contents as a result of osmotic pressure, combined with loss of cellular

membrane elasticity caused by cross-linking of protein molecules. However, simple breakdown or dissolution of lipid (without collapse of the cell) and its replacement by fixative of a higher density, would actually result in a weight gain. Baker (1958) noted that several workers have reported a gradual loss of lipids from tissues that are stored in formalin for appreciable lengths of time.

It is not clear why the other organs do not show an initial marked weight gain; indeed, the liver and kidneys rapidly lose weight. The existence of internal supporting tissue may mean that these organs are less susceptible to swelling. Freezing of carcasses before autopsy probably reduces osmotic effects, as membranes are disrupted by ice crystal formation (Pearse 1968).

Variation in weight changes between the left and right organs and perirenal fat was caused by their storage in different volumes of formalin. The right organs, stored in a larger volume of formalin relative to the weight of material immersed, maintained a consistently greater weight, regardless of whether the overall change was positive or negative. The left organs were stored with the much larger liver, which effectively reduced the amount of fixative available to other material in the container. Incomplete fixation of these tissues possibly rendered them more susceptible to solvent extraction, as formaldehyde is bound to proteins and therefore removed from solution during the fixation process.

Although interpretations of the events leading to the weight changes have not been rigorously tested, it is clear that fixation in formalin can affect calculation of indices of condition based on length and weight measurements. Parker (1963) demonstrated that significant changes in condition factors occur following fixation in formalin for several species of salmon (**Oncorhynchus**). Numerous studies on the physical condition of wild animals have used a fat index based on the ratio of perirenal fat weight to kidney weight, usually from fresh material or carcasses that have been stored by freezing (e.g. Riney 1955; Batcheler & Clarke 1970; Flux 1971). As both perirenal fat and kidney

weight are significantly affected by storage in formalin, correction factors must be applied if valid condition indices are to be calculated from preserved material. The same is true for other organs if they are to be used for comparisons of physiological or reproductive status.

If autopsy samples are to be preserved for later analysis, careful attention must be given to the volume of fixative used and length of storage. Parker (1963) has also shown that the concentration of fixative and ionic strength of the dilutant are important. Therefore, effort should be made to standardise, and record, all materials and methods used. Despite these disadvantages, the convenience of being able to store material, and the greater ease of handling, mean fixation is often a useful technique in wildlife studies.

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